University of Alberta

Spatial and temporal variability in white spruce (*Picea glauca*) cone production: individual and population responses of North American red squirrels (*Tamiasciurus hudsonicus*).

by

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In memory of my Uncle Danny LaMontagne

(April 25th, 1953 – February 27th, 2007)

ABSTRACT

Habitat quality is largely heterogeneous over space and time, although common simplifying assumptions in ecological research include homogeneity of areas occupied by a population and equal resource availability among individuals. These assumptions are made due to difficulties in quantifying the food available to individuals and following the effects of food on individual performance under natural conditions. My objectives were to document temporal and spatial variability in food availability, and its effects on seed predator individual performance and population dynamics in a white spruce – red squirrel system near Kluane Lake, Yukon. This system was ideal for my study because white spruce is the only conifer present, their seeds are the primary food for red squirrels, red squirrel populations can be completely enumerated, and individuals maintain non-overlapping territories. Models including spring population density and fall cone abundance best-fit red squirrel population growth rates compared to models including a 1-year lag in food abundance, or each term alone. Cone abundance influenced the population growth rate of red squirrels more than red squirrel density. Within years, cone availability varied spatially. Synchrony in cone production patterns of individuals showed spatial variation, although most trees produced large seed crops during a mast year. Fall red squirrel territory size was influenced by the age-class of the owner (adult or juvenile), the number of offspring weaned during the year, and population density. The number of cones in a red squirrel territory was influenced by the owner's age-class and cone availability near the primary midden. Overwinter survival was most affected by territory size, rather than cone availability, suggesting alternative food may be important when cones are low. However, female reproductive success was related to cone

availability in her territory. In low seed years, the highly skewed, unequal availability of food across territories suggests that spatial variation in food production, and consequently individual performance is important to short-term population persistence. Although assumptions of identical individuals have been long used in ecological research; here I have shown significant local variation in resource availability, and have provided insight into how important it may be in affecting individuals and populations in the wild.

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TABLE OF CONTENTS

CHAPTER 1. GENERAL INTRODUCTION & THESIS OVERVIEW 1
HETEROGENEOUS ENVIRONMENTS 1
RESOURCE AVAILABILITY 2
STUDY SYSTEM 4
THESIS CHAPTERS 5
LITERATURE CITED 8

CHAPTER 2. A VISUAL INDEX FOR ESTIMATING CONE PRODUCTION FOR INDIVIDUAL WHITE SPRUCE TREES 12
INTRODUCTION 12
METHODS 14
DATA COLLECTION 14
ANALYSIS 16
RESULTS 18
DISCUSSION 20
LITERATURE CITED 24

CHAPTER 3. DELINEATING MAST-SEEDING YEARS ACROSS SPECIES AND STUDIES: A GENERAL METHOD 32
INTRODUCTION 32
METHODS 34
DATA SETS 34
DELINEATION OF MAST YEARS 34
RESULTS & DISCUSSION 36
LITERATURE CITED 41

CHAPTER 4. EFFECTS OF FOOD AVAILABILITY AND CONSPECIFIC DENSITY ON RED SQUIRREL (*Tamiasciurus hudsonicus*) POPULATION DYNAMICS 56
INTRODUCTION 56
METHODS 60
STUDY AREA 60
POPULATION MONITORING 60
FOOD AVAILABILITY 61
MODELS 62
LIFE-TABLE RESPONSE EXPERIMENTS 64
RESULTS 65
POPULATION TRENDS 65
FOOD AVAILABILITY 66
MODEL FITS 66
LIFE-TABLE RESPONSE EXPERIMENTS 69
DISCUSSION 71
EFFECTS OF FOOD & DENSITY ON POPULATION GROWTH 71
VITAL RATE SENSITIVITIES & CONTRIBUTIONS TO POPULATION GROWTH .74
TERRITORIALITY & POPULATION DYNAMICS 76

Food limitation in red squirrels 78
LITERATURE CITED 81

CHAPTER 5. Local-scale variability and synchrony in mast seeding of white spruce 97
INTRODUCTION 97
METHODS 99
Study species 99
Data collection 100
Variability in cone production 101
Individual synchrony in cone production 101
Synchrony in mast and low cone production years 103
Temporal patterns of individual cone production 104
RESULTS 104
Variability in cone production 104
Synchrony in cone production 105
Synchrony in mast and low cone production years 105
Temporal patterns of individual cone production 106
DISCUSSION 107
Weather as a cue for synchrony 111
Pollination efficiency and predator satiation 113
LITERATURE CITED 116

CHAPTER 6. Intraspecific variation in territory size, territory quality & their effects on individual performance in red squirrels 129
INTRODUCTION 129
METHODS 133
Study area 133
Territory mapping 134
Quantifying cone availability 135
White spruce basal area distribution 135
White spruce cone production 136
Territory food levels 138
Analysis 138
Determinants of territory size & territory cone levels 139
Territory size, food resources, and individual performance ... 140
RESULTS 142
Territory size & territory cone levels 143
Reproductive success 146
DISCUSSION 147
Determinants of territory size & cone levels 148
Energetic requirements, available resources & alternative foods 151
LITERATURE CITED 156

CHAPTER 7. VARIATION IN INTRASPECIFIC FOOD AVAILABILITY TO RED SQUIRRELS: EFFECTS ON SURVIVAL, REPRODUCTIVE SUCCESS, & SHORT-TERM POPULATION PERSISTENCE 176
INTRODUCTION 176
METHODS 178
VARIATION IN CONE AVAILABILITY 179
CONES AVAILABLE TO INDIVIDUALS 179
Unequally distributed cones 179
Equally distributed cones 180
EXPECTED PERFORMANCE 181
RESULTS 182
DISTRIBUTION OF CONE RESOURCES AMONG INDIVIDUALS 182
PREDICTIONS OF OVERWINTER SURVIVAL & REPRODUCTIVE SUCCESS ... 183
DISCUSSION 185
LITERATURE CITED 191

CHAPTER 8. GENERAL DISCUSSION AND CONCLUSIONS 201
SUMMARY OF RESULTS 202
FUTURE RESEARCH 204
LITERATURE CITED 207

Appendix 1. The mean matrix for each population of red squirrels (A and B) based on transitions from 1990 to 2004 that was used for assessing sensitivity of lambda to variation in vital rates in life-table response experiments. 209

Appendix 2. Lower-level vital rates of female red squirrels fertilities in age-classes: (1) 1-year olds, (2) 2-year olds, (3) 3-4 year olds, (4) 5+ year olds. '...' cells show no individuals in an age-class, or no juveniles present for basing lower-level vital rates 210

Appendix 3. Predicted (grey symbols) and observed (black symbols) red squirrel population growth rates for two populations in the Yukon, Canada, from 1990-2004. Predictions were based on models including a) population density only (DD), b) food only (F), and c) both food and population density (DD+FL). 211

Appendix 4. The mean correlation index (± SE) showing the proportion of variation in P. glauca individual cone production patterns that was explained by cone production on another tree within a given distance class (see text for further information). 212

Appendix 5. Relationship between the number of territorial location points used to construct red squirrel territories and the resulting

territory size (n = 112) for analyses in Chapter 6. Solid symbols are for territories with ≥ 17 data points, open symbols have <17 data points. Only territories mapped with a minimum of 17 points are discussed in the text and used in analyses. 213

Appendix 6. a) Top panels show the trend of increases in mean individual white spruce cone production with increased basal area (2002-2005) in plots A (n = 207) and B (n = 261), and the high variability in cone production across the range of basal areas. b) Bottom panels show that there is little relationship between cone production per unit basal area and the basal area of the tree, this is especially the case for individuals with basal areas > 64cm^2 (9 cm dbh). 214

Appendix 7. Summary of territory size and number of cones in August territories of juveniles, adult males, and adult female red squirrels. Females are separated into non-breeders, those that bred but had no juveniles wean from the nest (failed breeders), and females that successfully weaned at least one offspring during the year. Means (standard errors) of raw and ln-transformed data are shown, with ranges of values in italics. 215

Appendix 8. Rank of white spruce cone abundance within red squirrel territories based on the age-class of the primary midden owner and the cone density in 0.1 ha surrounding the midden. Populations were in two study plots (A & B), and experienced three low cone years (2002-2004) and one mast year (2005). Y-axes are the estimated cones within each territory, note that 2005 is on a different scale; X-axes are the rank of cone abundance and vary due to fluctuations in population size. The horizontal line is at 7300 cones, half of the estimated overwinter energy requirement (Humphries et *al.* 2005; Chapter 6). 216

Appendix 9. Fit of gamma or exponential distributions (lines) to the number of cones in red squirrel territories (bars). Exponential distributions are shown for A-2003, A-2004, and B-2004, the remainder are gamma distributions. 217

LIST OF TABLES

Table 2-1 Published conversion values for total cone crop estimation from cone index methods. "y" = the actual total number of cones on a tree after felling (unless otherwise indicated), and "x" = the binocular count of all cones from one side of the tree. Other parameters used are indicated. "None" indicates that the conversion factor was determined based solely on assumptions about the crown shape and openness, or the size and/or position of cones in the crown. 28

Table 2-2 AIC_c comparisons of predictions based on an independent test data set of total cones produced from a range of cone conversion factors found in the literature (Total cones = Cone index · 1.5, Total cones = Cone index · 2.0), the average ratio of index to actual cones based on my data set (3.35), and the conversion presented here (log(Total cones) = 0.073 + 1.189 · log(Cone index)). Akaike weights (w_i) are probabilities that model 'i' is the best fit of the candidate models and only for the data upon which they are evaluated and range from 0 to 1 (Burnham & Anderson 1998). Bold shows the model with the highest w_i value..... 29

Table 3-1 Data-sets used in analyses of mast years, ranked by increasing values of CV among years. Letters after species names represent different sites within a study. 'n' is the number of years of seed production data, 'Data' is the type of seed data collected (see footnote), 'Mean' refers to the mean number of seed produced in the data-set (see 'Data' for units of seed production), 'SD' is the standard deviation of seed production

over time, 'CV' is the coefficient of variation of seed production among years. 45

Table 4-1 Population models fit to data. 'N' is the spring female red squirrel population density (per ha^{-1}), and 'F' is white spruce cone crop density recorded in July (per ha^{-1}) of years '$t-1$' and 't'. 90

Table 4-2 AIC_c results and Akaike weights (w_i) for population dynamics models based on female-only red squirrel population growth for a) population A and b) population B. See table 4-1 for the explanation of the models. The "Rank" score is based on w_i . 'n' is the number of parameters in each model, and R^2 is the fit of the predicted and observed population growth rates. 91

Table 4-3 Parameter estimates of the best-fit model, density and food (DD+F), with the highest AIC_c weights in model fitting, and the density only (DD) and food only (F) models for red squirrel population growth rate. Values in brackets are the 95% confidence interval. See Table 4-1 for the form of the models. 92

Table 5-1 Number of years of data for each of the study plots (n), and for each plot, the coefficient of variation (CV_p), the mean spearman correlation for synchrony of pairs of trees ($\overline{r_s}$), the mean CV for individuals in each plot ($\overline{CV_i}$), and the autocorrelation function value (ACF_t; 't' represents the lag in years) and standard error. The maximum ACF lag calculated was approximately three times shorter than the data series. See text for number of individuals in plots. 121

Table 5-2 Final model from multinomial logistic regression for dominant ACF lags. Individual trees with a negative lag at 1 year, or a positive lag at 3 years were compared to trees with no significant lag. 'n' is the number of individuals with each pattern. Trees with dominant lags of 2, 4 and 5 years were omitted from this analysis; they comprised only 10% of individuals sampled. 122

Table 6-1 Stepwise and main-effects models of factors influencing ln(red squirrel territory size (m^2)) with the number of parameters (n_i), ΔAIC_c, AIC_c weights (w_i) and R^2. Age-classes are 'adults' or 'juveniles', mass is the lowest mass recorded in August (g), density is conspecific density, BA density is the basal area of spruce >5cm dbh in a 0.1ha buffer of the primary midden, cone density is ln(total cones in the 0.1ha buffer). 165

Table 6-2 Parameter estimates for the best red squirrel territory size model (ln(red squirrel territory size (m^2)). Standard errors are robust errors adjusting for repeated sampling of focal middens. 166

Table 6-3 Stepwise and main-effects models of factors influencing the total number of white spruce cones in a territory, quantified as ln(total number of cones in territory). See Table 6-1 for explanation of table contents. 167

Table 6-4 Parameter estimates for the best model of the cones contained in red squirrel territories (ln(total number of cones within territory)). Standard errors are robust errors adjusting for repeated sampling of focal middens. 168

Table 6-5 Mean (± SE) attributes of fall territory size and territory cones for individuals that survived overwinter, and of the adult females surviving overwinter, the same attributes for females producing a litter, having one or more juveniles emerge from the nest, and having one or more juveniles successfully wean. T-tests were conducted for overwinter survival, with a two-sided test for territory size, and a one-sided test for cones in the territory; and one-sided tests for reproductive performance. One-sided tests were used for female performance, to test if females that performed better had access to more cones on average than individuals that performed poorly. 169

Table 6-6 Logistic regression results of models for the influence of territory size (ha) and territory cone quality (estimated total number of cones in territory) on overwinter survival and adult female spring reproductive success (producing a litter, having juveniles reach emergence). 170

Table 6-7 Logisitic regression parameters and odds-ratios with 95% confidence intervals for the best models based on AIC_c weights influencing red squirrel overwinter survival and adult female spring reproductive success (producing a litter, having juveniles reach emergence). Models include either territory size (ha) or territory cone quality (estimated total number of cones in territory in 10000's). 171

Table 7-1 Summary of the mean (per-capita) cones per individual and the range of cones per individual red squirrel territory, and the proportion of

individuals exceeding thresholds for overwinter survival and female reproductive success. The thresholds for overwinter survival (7300 cones), and for adult female reproduction the following spring (9200 cones for juvenile emergence from the nest based on adult females only (ratio of successful females / total females shown)). 'N' is the population size each year. Bold shows when the proportion based on per-capita cones is zero. 196

Table 7-2 Summary statistics for normality and skewness tests of the distribution of white spruce cones among individual red squirrels in the southwest Yukon, in each of 2002 to 2005. When the skewness statistic is greater than 2 times the standard error of skew (SES) there is significant skew present. 197

LIST OF FIGURES

Figure 2-1 The model data set (n = 40, black symbols) and test data set (n =20, grey symbols) for the white spruce cone calibration, showing the relationship between log(cone index) and log(actual total cones) for trees used in regression analysis. Diamonds represent data collected in the Yukon (2002, 2003, 2004) and the Alberta data (1999) data by circles. The regression line is the fit of the log-log conversion created here to the model data set, y = 0.073 + 1.189x (R^2 = 0.94). 30

Figure 2-2 Observed and predicted actual total cones from each the four models in Table 2-2 (open circles represent predictions based on: cone index · 1.5, triangles: cone index · 2.0, squares: cone index · 3.35, and black diamonds: 0.073 + 1.189 · log(cone index)). Panels 'a' and 'b' show the fits of the model data set for log-transformed and back-transformed data, respectively, and panels 'c' and 'd' show the fits for the test data set. The 1:1 line represents that observed and predicted cone abundances are equal (a perfect model). Note that the scale of the axes varies among panels. 31

Figure 3-1 Measurements of mean annual seed production for 36 data sets (left panel), their ranked distribution of seed (centre panel), and variation in annual means shown as the number of standard deviations from the long-term mean (right panel). Years identified as mast-seeding years based on the standardized deviate method are indicated by solid

symbols and bars. Horizontal dashed lines represent the long-term mean seed production across years for each data-set. Data-sets are ordered by increasing CV among years. Note: species, site (if applicable) and CV are indicated in the subheadings. Y-axis variables in the first 2 panels vary and are indicated for each plot; in the centre panel the seed output years are ranked from high to low, rank appears in the x-axis. See Table 3-1 for more information. 48

Figure 3-2 The minimum standardized deviate for the 36 seed production data sets increases with increases in CV. 55

Figure 4-1 Schematic of the relationship of variables input into the population models $N_{i,t}$ is the spring female red squirrel population density (per ha) of population 'i' in year "t", $N_{i,t+1}$ is the spring population density in year "t+1". $F_{i,t-1}$ is the mean number of cones produced per ha in the summer of year "t-1" within the area occupied by population 'i', and $F_{i,t}$ is the mean number of cones produced per ha in the summer of year "t". The growth rate of population 'i' was calculated as $\ln(N_{i,t+1}/ N_{i,t})$. 93

Figure 4-2 Time series (top panel) and population growth rates (lower panel) for two red squirrel populations in the southwest Yukon (1990 - 2004). Data are based on spring (May) censuses of female red squirrels. 94

Figure 4-3 Abundance of white spruce cones present on trees (# cones·ha^{-1}) based on visual counts of sample trees and the density of mature white spruce on each study grid from 1989-2003. 95

Figure 4-4 Annual mean spring territory sizes of female red squirrels sampled

from a 9ha area of plot B from 1990-2004. At least 11 territorial locations were used in generating 100% minimum convex polygon territory sizes. Within each year there was no significant effect of the number of mapping points on territory size. The horizontal line is the long-term mean and number above each bar shows the number of territories mapped (Boutin, unpublished data). 96

Figure 5-1 Study plot locations for *P. glauca* synchrony in cone production, Yukon, Canada (61°N, 138°W). The line in the map represents the Alaska Highway. 123

Figure 5-2 Mean annual *P. glauca* cone production for each study plot from 1990 (or 1991) to 2005 in the Yukon, Canada (left panels). The dashed line is the long-term mean cone production. Right panels show the number of standardized deviations the annual cone production mean was from the long-term mean. Filled symbols/bars represent mast years based on deviations in cone production from the long-term mean (see methods). 124

Figure 5-3 Annual coefficient of variation (CV_A; bars) with mean annual cone production (line), for each of the study plots: A (n = 83), B (n = 84), C (n = 84), and D (n = 105) from 1990 - 2005. 125

Figure 5-4 Spatial variation in synchrony of cone production by *P. glauca* pairs of individuals. The vertical line is where distances between tree pairs generally move from within to between study plots. All mean correlations for each distance class were significantly greater than

zero and less than one. 126

Figure 5-5 Percentage of *P. glauca* trees that produced large cone crops within each year. Only trees in the data set for at least 13 years were included in analysis. Large cone crops were defined as the number of mast years that occurred at the plot scale (see Figure 5-2). Plot A (n = 66) and B (n = 61) have their top 3, plot C (n = 55) has its top 2, and plot D (n = 14) has the single top cone year shown. Solid bars represent the top cone year, angled lines represent the year with the second highest number of cones, and dotted bars represent years with the third most cones, when shown. Recall that data for plots C and D span 1991-2005 only, and no data are available for plot D in 1996 and 1997. ...127

Figure 5-6 Percentage of *P. glauca* trees producing their lowest cone crop within each year for each of the four study plots. Only trees in the dataset for a minimum of 13 years were included in the analysis. The lowest cones may occur in more than one year for each tree. Sample sizes are the same as in Figure 5-5. Recall that Plots C and D span 1991-2005 only, and no data was available for plot D in 1996 and 1997. 128

Figure 6-1 Spatial and temporal variation in pre-caching white spruce cone density (cones · $10m^{-2}$) in 2002 to 2005. Plot A is at the top, B at the bottom (indicated in first panel). Note that legend scales differ among years. White shows low, and darker greys and black showing the areas of higher cone production in each year. 172

Figure 6-2 Territory sizes and the total number of white spruce cones contained

within individual red squirrel territories mapped in late-July to mid-August, 2002 to 2004. Lines show the linear relationship in each year. Annual data are shown as filled squares (2002, n = 21), light grey circles (2003, n = 32), and dark grey diamonds (2004, n = 40). 174

Figure 6-3 Relationship between territory size and the total number of white spruce cones contained within the territory and whether individuals survived (solid symbols) or did not survive (open symbols) overwinter, measured as surviving until the May midden census (n = 93). Data for all years is shown as squares (2002), circles (2003), and diamonds (2004). 175

Figure 7-1 Spatial distribution of white spruce cone resources in each of 2002 to 2005. The legend represents the number of cones per $10m^2$ cells and the scale varies each year. The black circles show the location of all primary red squirrel middens within each study area each year. Population A is on the upper right and B is the lower panel. 198

Figure 7-2 Frequency distribution of cones in individual red squirrel territories in two populations, A and B, from 2002 to 2005. Note that the x-axis and y-axis scales vary. The dashed line represents 7300 cones; based on energetics this is the minimum number of cones required for overwinter survival when cones comprise 50% of the diet. 200

CHAPTER 1

GENERAL INTRODUCTION & THESIS OVERVIEW

HETEROGENEOUS ENVIRONMENTS

Organisms live in heterogeneous environments, variable in both time and space (Stewart et *al.* 2000; Strayer et *al.* 2003). The availability of resources such as food is crucial to ecological processes, but food levels are often poorly defined and quantified (Abrams 1988). Regardless of the reality and relevance of environmental heterogeneity, in population ecology studies it is often assumed that resources are distributed homogeneously, and that individuals within a population are identical with equal access to these resources (Kingsland 1985; Wiens 2000). At the population level, density alone is often used to describe changes in population dynamics, with density representing the per-capita availability of food to individuals (Begon et *al.* 1996). This is an inaccurate representation of the food available to individuals because natural environmental variability may cause substantial temporal and spatial variability in food availability independent of population density. This simplification is justified only if variation between individuals is very small, with insignificant effects on ecological processes. It is well documented that individual performance (survival, reproduction) is linked to food abundance, and has been shown in food supplementation experiments (Boutin 1990; Adams 2001). Furthermore, individual variability is the basis of the most general ecological theory, natural selection (Łomnicki 1988).

Although these assumptions simplify the interpretation of relationships between individuals and their resources, and classic population models using state variables (e.g.,

population size or population density; Lotka 1925, Volterra 1926, Nicholson & Bailey 1935) have produced general principles, there is a tradeoff between generality, realism, and precision (Levins 1966). It had been argued that incorporating more environmental and individual variation would create more realistic understandings of ecological patterns (Grimm & Railsback 2005).

Heterogeneity in habitat quality has often been investigated at coarse-scales, for example, as different vegetation-based habitat patches (Ferrer & Bisson 2003; Kerbiriou et *al.* 2006), while within a habitat type homogeneity is assumed. Very few studies have quantified resources within an individual's territory (Gill & Wolf 1975; Kodric-Brown & Brown 1978; Nagy & Holmes 2005). Little is known about the relationship between an individual's territory size and territory food levels, *within* a habitat-type, and how they affect components of their fitness (survival, reproduction). It has been shown that the 'quality' (i.e., resource levels) associated with a particular habitat type is not necessarily consistent, at least temporally (Wheatley et *al.* 2002). Within a habitat it may also be the case that not all areas are of equal quality.

RESOURCE AVAILABILITY

Intraspecific competition for resources leads to resource partitioning that is broadly categorised into scramble or contest competition (Nicholson 1954; Varley et *al.* 1973). In scramble competition, resources are used simultaneously between individuals and their direct interaction makes competition balanced, resulting in a gradual decline of the population growth rate with a decrease in the amount of resources. Contest competition includes dominance hierarchies or territories (Morse 1980). Given that

resource levels affect individual fitness, individuals should aim to secure resources, often excluding others through defending a territory (Adams 2001) or being dominant (Morse 1980). Territoriality is a form of contest competition that has likely evolved in response to the distribution of food, and occurs when it is beneficial for individuals to defend access to food resources or mates (Brown 1964). Territories can be established such that resources are divided equally among individuals within a population who then have equal fitness (Fretwell & Lucas 1970) or unequally among individuals (Kodric-Brown & Brown 1978). Individuals may adjust their territory size such that all individuals have equal access to resources, or resource partitioning may be unequal due to competitive differences among individuals (Łomnicki 1988).

Given heterogeneity in the distribution of resources not only between but also within habitat types, variation in the performance of individuals (e.g., fecundity, survivorship) *within* a population should be expected (Nilsen et *al.* 2004). A limitation in investigating the effects of variability in the availability of food on both populations and individuals in nature has been due to the difficultly in quantifying food available at both the population level and among individuals (Łomnicki 1988; Boutin 1990). Variation in the performance of individuals due to unequal food partitioning can lead to different population dynamics including predictions for population persistence (Łomnicki 1988) compared to if all individuals were identical.

The goal of my thesis research was to investigate natural variation in food availability and how it affects the quantity of resources acquired by individuals, their performance, and ultimately population dynamics. I approached this problem by not only studying the consumer population, but also examining the temporal and spatial variability

in the availability of the primary food source. My research was also conducted in a single habitat type; therefore I was investigating finer scale variation in food resources rather than variation across habitats. I had four main objectives: 1) to compare the relative and combined effect of food availability and population density on population dynamics, and identify the vital rate that contributed the most to population growth; 2) to quantify the spatial and temporal variation in resource production patterns; 3) to examine determinants of territory size and territory resource levels and how these affected individual performance (survival, reproduction); and 4) to examine how the distribution of food in individual territories compares to equal per-capita food levels, and expected performance of individuals based on these divisions of food.

STUDY SYSTEM

Red squirrels (*Tamiasciurus hudsonicus*) are arboreal sciurds found throughout the boreal forest of North America (Steele 1998). They are highly territorial and occupy individual, non-overlapping, year-round territories (Gurnell 1984). ~~In con~~iferous forests, individual red squirrels cache cones in a centrally placed hoard within their territory called a midden; individuals can cache thousands of cones annually (Smith 1968). A territory with a supply of cones in a midden is required for overwinter survival (Smith 1968; Steele 1998). Offspring are typically born between March and June, and wean at about 70 days of age; they either disperse to establish a territory or settle on a portion of their mother's territory (Boutin & Schweiger 1988). Individuals rarely move to another territory once they have become established (Price et *al.* 1986). White spruce (*Picea glauca*) is the only conifer species in the study area (Dale et *al.* 2001), and undergoes

large temporal variation in the size of cone crops, known as mast seeding (Kelly 1994). Seed production of white spruce is influenced by the size of the tree (Greene et *al.* 2002), its local environment (e.g., basal light, Greene et *al.* 2002), available nutritional reserves (Nienstaedt & Teich 1972), and regional weather patterns (Selås et *al.* 2002). The remaining cones open in fall to release their seed and the open cones fall off the tree overwinter.

This is an ideal system for examining the relationship between food availability and conspecific density on population dynamics, and assessing the consequences of variation in the availability of the primary food resource among individual territories on their performance. White spruce cones are produced annually on trees and are easily identified by sight while ripening on trees in July and August prior to being clipped and cached by red squirrels (Peters et *al.* 2003). White spruce cones can also be quantified on individual trees (Chapter 2; LaMontagne et *al.* 2005), over time and space. Red squirrels are readily habituated to observers (Vlasman & Fryxell 2003), are easily uniquely marked, and make conspicuous territorial 'rattle' calls (Price et *al.* 1986); this enables the territories of individuals to be mapped. The nests of red squirrels are relatively easy to access, allowing for litter size of individuals to be determined and the fates of offspring to be followed beginning at birth. Because of their territorial nature, the entire population of red squirrels within an area can be completely enumerated.

THESIS CHAPTERS

This study is comprised of six data chapters. Chapter 2 is "A visual index for estimating cone production for individual white spruce trees". In this chapter (also published as

LaMontagne et *al.* 2005) I described a method for generating an index of the number of cones present on trees and provide an empirically derived equation that allows the index to be converted into an estimate of actual number of cones produced on a tree. This method was important for quantifying the total number of cones on trees when assessing the total number of cones available on red squirrel territories, and was routinely used in other chapters.

In Chapter 3, "Delineating mast-seeding years across species and studies: a general method", I reviewed a series of potential methods to quantitatively define a mast year, and suggest an objective method to quantify mast years. In doing so, I examined a variety of plant species and sampling techniques used to measure seed production. The intent was to capture the qualitative descriptions of the quantity of seed produced within mast years. Therefore, when white spruce cone production was referred to as a "mast year" in the thesis, it was based on the objective criteria described here.

Chapter 4 is "Effects of food availability and conspecific density on red squirrel population dynamics". I tested the predictions that the population growth rate of a territorial species living in a temporally variable food environment would be influenced most strongly by i) population density, ii) food availability or iii) a combination of these. A series of statistical models were fit to time-series data of red squirrel population growth rates over 15 years. I used life-table response experiments (LTRE; Caswell 1989) to investigate the response of the population growth rate to temporal variation in fertility and survival in four age-classes (yearlings, 2 year-olds, prime-age (3-4 years), and older (5+) individuals). My working hypothesis was that red squirrel population growth rates are a function of both conspecific density as well as food availability.

Chapter 5, "Local-scale variability and synchrony in mast seeding of white spruce", demonstrated the temporal and spatial variability in white spruce cone production patterns by individual trees. Using a data set including cone production records of up to 16 years for over 350 trees, I addressed two general questions: 1) How variable was cone production between and within years? and 2) How synchronized were patterns of cone production between trees? Based on the concept of mast seeding, I expected high variation in seed production between years within a population, and individuals to have similar patterns of seed output, hence little variation, within a year. I also expected high synchrony in seed production patterns of individuals over time. If there was considerable variation in the cone production patterns of individuals over time this may give rise to spatial variation in the availability of cones with implications for the performance of individual red squirrels in the population.

Chapter 6 is "Intraspecific variation in territory size, territory quality, and their effects on individual performance in red squirrels". For this chapter I examined the relationship between spatial and temporal variation in food availability and individual attributes on their resulting territory size and food resources contained within the territory. In addition, I tested the relationship between territory size and resource levels. I tested the hypotheses that 1) territory size was dictated by local food availability, or, that 2) territory size and resource levels were a function of population density or other individual or local habitat attributes, and that 3) territory resource levels were significantly related to an individual's performance, specifically their ability to survive overwinter and (for females) their reproductive success the following year compared to no influence on individual performance.

In Chapter 7 "Variation in intraspecific food availability to red squirrels: effects on survival, reproductive success, & short-term population persistence" I used the model developed in Chapter 6 to infer the number of cones available to each red squirrel in the population and I examined the distribution of white spruce cones among individual red squirrel territories. I compared the distribution of white spruce cones among years and the predictions for individual overwinter survival within a population based on the distribution of cones among individuals compared to mean per-capita cone levels, and compared expectations for short-term population persistence.

Together, these chapters provided unique insight into the variability in resources available to individual within a natural population. This included examining the temporal and spatial distribution of resources (synchrony in cone production between individual white spruce trees and mapping the spatial distribution of cone production throughout the study area); I examined the distribution of resources among individuals and their performance, and I scaled this variability back up to potential effects on short-term population persistence. In the final chapter I summarized the results and raise a series of additional questions based on the work done here.

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CHAPTER 2

A VISUAL INDEX FOR ESTIMATING CONE PRODUCTION FOR INDIVIDUAL WHITE SPRUCE TREES

INTRODUCTION

Cone crop data are used to model tree productivity (e.g. Greene et *al.* 2002, Calogeropoulos et *al.* 2003), and as an explanatory factor in studies of conifer seed predators (e.g. Holimon et *al.* 1998, Humphries & Boutin 2000, McAdam & Boutin 2003). Stand-level cone crops are typically based on a qualitative assessment of the relative number of cones on trees and the number of cone-bearing trees within a stand (Eremko et *al.* 1989). For instance, to assess the relative size of the cone crop in the interest of cone collection for provincial reforestation programs, cone crop ratings can vary from "no cones" (crop rating: 1 or none) to "many cones on almost all of the trees" (crop rating: 7 or very heavy) (Eremko et *al.* 1989). This method does not achieve the level of detail required when a researcher is interested in quantifying cone production by individual trees within an area. In addition, monitoring the same individual trees each year reduces the among-year variation due to differences in individual quality, increasing the accuracy of between-year comparisons (Koenig et *al.* 1994). Estimating total cone crop through non-destructive sampling, specifically by assessing total cone number by an index of visible cones from one side, is a standard way to monitor cone production when quantitative information is required (e.g. Holimon et *al.* 1998, Turkington et *al.* 1998, Humphries & Boutin 2000, Greene et *al.* 2002, McAdam & Boutin 2003, Peters et *al.*

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2003), and is desirable when monitoring long-term cone and seed production and availability within an area.

An index value is typically assumed to be a close surrogate for total numbers (Anderson 2001), but conversion factors may be developed to quantify the relationship allowing total numbers to be predicted. Conversion factors of between 1.5 and 3.0 have been used to estimate the total cone production from the index of visible cones for a variety of tree species (Table 2-1) including loblolly pine (*Pinus taeda* L.; Wenger 1953), slash pine (*Pinus elliottii* (Engl.); Hoekstra 1960, Webb & Hunt 1965), and Douglas fir (*Pseudotsuga menziessii* (Mirb.) Franco; Garman 1951). These conversion factors were based on cone counts before and after felling, or from cone collections from commercial tree climbers. However, other conversion factors are based solely on assumptions, and not on empirical data. For example, Fowells & Schubert (1956) and Franklin (1968) proposed that counting the number of visible cones from one side of a tree and then multiplying this value by 1.5 accounted for the cones on the non-visible portion of the tree. This was based on the assumption that two-thirds of the crown was visible (Franklin 1968), and it was thought that this method gave a reasonable estimate of the total number of cones per tree for sugar pine (*Pinus lambertiana* Dougl.), ponderosa pine (*Pinus ponderosa* Dougl. ex Laws), and white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr). Although this assumption may hold for conifer species with open crowns, large cones, and/or those that do not produce large cone crops (e.g. sugar pine), it may not be true for species with dense crowns or when cone crops are heavy. In this study I describe a simple method for indexing the number of cones present on white spruce (*Picea glauca*) and provide an empirically derived equation that allows the researcher to convert

the index into an estimate of actual number of cones produced. I compare the accuracy of my conversion equation with others described in the literature.

METHODS

DATA COLLECTION

White spruce trees produce new green or purple female cones in mid-summer, with these non-serotinous cones opening in fall to release seeds and the empty cones typically falling from the trees during winter. I visually estimated the number of cones on individual white spruce trees at a study site in the boreal forest region in the southwestern Yukon for three years (61°N, 138°W; 2002: n (number of individual trees) = 21; 2003: n = 11; 2004: n = 8), and used data from Peters et *al.* (2003) for one year in the mid- boreal mixedwood ecoregion in northeastern Alberta (55°N, 112°W; 1999: n = 20). All trees sampled had a diameter at breast height of > 5cm, the size at which white spruce trees may begin to produce cone crops (LaMontagne & Boutin, unpublished data). All sampling was conducted in July, prior to cone harvesting by red squirrels (*Tamiasciurus hudsonicus* (Erxleben); Peters et *al.* 2003).

To obtain the cone index, observers stood with the sun behind them and far enough away from the tree such that the area of the crown where female cones are produced (typically the top one-third of the crown for white spruce; Eremko et *al.* 1989, Turkington et *al.* 1998) could be clearly seen. Trees were selected based on the visibility of the tree crown (i.e. an unobstructed view) and to capture the range of cones produced by white spruce. Mean tree height near the Yukon study area was 9.2m (LaMontagne & Boutin, unpublished data) and observers stood approximately15-20m away from the base

of the tree. Near the Alberta site, mean tree height was 20.0m (Peters et *al.* 2003), with observers at distances of 20-40m (Susan Peters, personal communication). The index of cone production was based on a count of all cones visible from one side of the tree, using binoculars (Fowells & Schubert 1956, Franklin 1968, Turkington et *al.* 1998, Peters et *al.* 2003). While counting, the observer did not change position. When the number of cones on a tree was visually assessed to be < 100, 3-5 observers determined the index of cone production by counting cones, and the average value was taken to be the index. For these counts the range of values by observers did not differ from the mean by more than ± 16 cones. For the purposes of generating the conversion factor multiple observers were used in order to minimize individual bias, however, a single well-practised observer, or observers could implement this method alone. With multiple observers conducting the index on trees independently, during training their index estimates should be compared such that all data can be used. When > 100 cones were visible, a photograph of the tree was taken using a 200 - 300mm telephoto lens and 100 or 200 ISO colour film. Cones were counted from 10cm x 15cm photographs with the aid of a magnifying lens. The image of each cone was poked with a needle to avoid double counting. All trees from 1999 were photographed, as all trees had > 100 cones, with the cone coverage of the crown extending lower than the top one-third of the crown in some cases. After the cone index was determined, or the photograph taken, the tree was felled, and all cones were removed from the tree and counted. If any cones were dislodged during felling they were collected from the ground and included in the total cone counts for the tree.

ANALYSIS

Prior to analysing the relationship between the cone crop index and actual cones the data were stratified into the lower and upper halves of the data range. Then the data were partitioned, with two-thirds of the data (40 trees) selected from which to construct the relationship (the model-set) and the remaining one-third of the data (20 trees) used for testing the relationship (the test-set; see below). Trees were randomly selected for each group such that half of the data for each set originated from data within the lower half of the range of the cone index values, and the other half from the upper half of the data range. This was done to ensure that both model and test data-sets covered approximately the same range of values. All raw cone data were log (base 10) transformed prior to analysis, to meet the assumptions of linear regression (Sokal & Rohlf 1995). The relationship between the log (cone crop index) and log (actual total cones) was determined using linear regression.

I compared my log-log conversion factor constructed here to results obtained by two commonly used conversion methods, those of Fowells & Schubert (1956) and Franklin (1968), and Wenger (1953). To do this, the raw cone index of both the 40 trees in the model-set and the 20 trees in the test-set were each multiplied by 1.5 and 2.0, respectively, to obtain an estimate of total cones, and then log transformed. I also estimated total cones based on the mean ratio of untransformed cone index : untransformed actual total cones from trees in the model-set for comparison. This ratio method provides a conversion factor similar to the ones produced by the other methods (e.g., the 1.5 and 2.0 conversion factors of Fowells & Schubert (1956), Franklin (1968), and Wenger (1953)). The mean ratio of untransformed data was calculated so that I

could compare a linear conversion factor based on white spruce to the log-log model (representing a non-linear conversion). A linear regression was not conducted on the untransformed data because the assumptions of constant variance and of a linear relationship between the variables were violated.

Akaike's Information Criterion calculated using maximized log-likelihood (Burnham & Anderson 1998) with small sample bias adjustment (AICc; because the number of data points per parameter in a model ranged from 10 to 40; Hurvich & Tsai 1989; Table 2-2), was used to compare the fit of the following models to the actual cone production data: a) the log-log regression model constructed here, b) the ratio method of cone index : actual cone production data, c) cone index · 1.5 (Fowells & Schubert 1956, Franklin 1968), and d) cone index · 2 (Wenger 1953). AICc values rank the relative ability of a suite of models to fit a common set of data and prefers parsimony, but do not provide information on the absolute fit of a model to data (Burnham & Anderson 1998). The model with the lowest AICc value is typically the most plausible model for the data, although as a rule of thumb models with an AICc difference (for model 'i': $\Delta AICc_i = AICc_i - AICc_{min}$; where 'min' is the minimum AICc value) of ≤ 2 do not allow the selection of one model over another. Models with a ΔAICc value of 4 to 7 have less support, and models with a ΔAICc >10 have essentially no support or explain very little of the variation in the data compared to the other models (Burnham & Anderson 1998). I calculated Akaike weights from the ΔAICc values to determine the best model, as they are considered as the weight of evidence for a model compared to other models estimated for a given set of data, and range between 0 and 1 (Burnham & Anderson 1998). AICc and AICc weights were calculated for all four models (a – d) on both the model-set and

the independent test-set of data, and with both log-transformed and back-transformed (or untransformed) data, since both of these scales may be useful in silvicultural and ecological studies. I examined the fit of each of the models by comparing the observed data on total cones and model predictions.

RESULTS

The years of study included three years of relatively low cone production (2002, 2003, 2004; mean cone index = 50, 13, and 15 cones, respectively; LaMontagne & Boutin, unpublished data), and one year of moderately high cone production (1999; mean cone index = 288 cones; Peters et *al.* 2003) in the study areas. Temporal variation in cone production is not explored here; these data were used because of the large range in the number of cones produced. The range of cone index values for all of the white spruce tree cone count conversion data collected (n = 60) was from 7 to 1 778, and the range in actual total cones was 8 to 18 621 (Figure 2-1). The mean ratio of the untransformed cone index : untransformed actual total cones was 3.35 (range: 1.14 – 10.92) for the model data-set, and 3.59 (range: 1.12 - 10.39) for the test data-set. There was no significant difference in the mean cone index : actual cone ratios of the untransformed data in the model-set and test-set (Two sample t-test, t = - 0.411, df = 58, p = 0.683).

The log-log regression model of the cone index to actual total cones constructed using the model data set was:

$$\log(\text{actual total cones}) = 0.073 + 1.189 \cdot \log(\text{cone index})$$

The intercept, with a standard error of the estimate of 0.017 was not significantly different from zero (p = 0.490), conversely, the slope with a standard error of the estimate

of 0.008 was significantly different from zero ($p< 0.001$). This model explained almost all of the variation in the data, with an R^2 value of 0.94. Residuals of the log-log regression were not significantly different from normal (Kolmogorov-Smirnov test, maxdiff = 0.151, $n = 40$, $p = 0.323$).

AICc analyses demonstrated that for both the model and test data-sets, my log-log model was the best at fitting the relationship between the cone index and actual total cones (Table 2-2). AICc weights were consistently above 0.90 for the log-log model. This model outperformed the ratio of cone index : actual total cones; consistently ranked as the second-best model, with the log-log model minimally ten times more likely to be the best model of all those tested (Table 2-2). The Wenger (1953) conversion (cone index · 2) was consistently ranked third, and the Fowells & Schubert (1956) and Franklin (1968) conversions (cone index · 1.5) ranked last of the models tested. In addition, the log-log model consistently provided the best fit to the cone production data, regardless of whether the data were preserved in the log format, or back transformed to actual cone numbers (Table 2-2, Figure 2-2). I ran multiple partitions of the data (multiple random selections of model and test data-sets) to ensure robustness of my results; in all cases the parameters of the log-log model and value of the cone index : actual cones were similar (LaMontagne, unpublished data).

Predictions of log(actual total cones) from the log-log model were consistently closer to log(observed cones) than the other models tested for both the model and test data-sets (Figure 2-2). While the predicted number of log(cones) was similar for cone index · 1.5 (Fowells & Schubert 1956, Franklin 1968), cone index · 2 (Wenger 1953), and the log-log model at low cone abundances (< log(1.5) cones), the ratio method (cone

index · 3.35) predicted more cones than observed up to about log(2.5) cones. Generally, as log(observed cones) increased, the predicted cone abundance from the other models grew increasingly poorly from the observed cone abundance compared to the log-log model (Figure 2-2c). This is even clearer for back-transformed cone numbers, where the predicted cones from the Fowells & Schubert (1956) and Franklin (1968) conversions (cone index · 1.5) level off at 1100 cones, and 1500 cones for the Wenger (1953) conversion (cone index · 2; Figure 2-2b), when the actual cones are 2500 to 8000. Similar deviations from the observed number of cones are seen with the test data-set (Figure 2-2d). Predictions from the log-log model were consistently closer to the observed total number of cones; however, all models increasingly under-predicted the total number of cones at very high cone abundances.

DISCUSSION

Neither the Fowells & Schubert (1956) and Franklin (1968) methods of conversion from a cone index (cone index · 1.5 = the total number of cones), nor the Wenger (1953) method (cone index · 2.0) performed well at predicting white spruce cone abundance, when compared to the log-log model outlined here. Using a multiplier of 1.5 or 2.0 generally underestimated the ratio of the cone index to the actual total cones for white spruce, which I found to be on average 3.35. Fowells & Schubert (1956) suggested that their conversion factor of 1.5 for a variety of *Pinus* spp. was subject to some error and that this likely varied according to species, with the species having large cones (e.g. sugar pine) likely being more closely approximated using their conversion. However, for species with smaller cones and cone placement occurring in clusters and close to

branches and twigs (e.g. ponderosa pine and white fir) they suggested that the error would be greater, as it would be difficult to see the same proportion of cones. White spruce has a much denser crown than many of the pine species (Oswald & Nokes 1988), therefore, it is not entirely surprising that the low conversion factors designed for pine species did not perform well for white spruce. Furthermore, for the log-log conversion the y-intercept value was positive as would be expected, because a negative intercept would indicate that an observer is counting cones as an index that do not actually exist, which is not possible. I suggest that '1' be added to any cone index values of zero prior to log-transformation, following Underwood (1997). Therefore, the predicted value of log(actual total cones) when the index is zero is equal to the intercept of 0.073, which is a predicted back transformed actual cone value of 1.18 cones.

In addition, the conversion factor of cone index · 1.5 (Fowells & Schubert 1956, Franklin 1968) was based solely on assumptions about the ability to view cones, and not any actual tree-felling data (Table 2-1). Conversion factors based on visible-cone counts and felling of loblolly pine (Wenger 1953, Wasser & Dierauf 1979) and slash pine data (Hoekstra 1960, Webb & Hunt 1965) show conversion factors in the range of 2 to 3, still below the ratio of cone index : actual cones for white spruce shown here.

Another consideration in determining a suitable cone conversion factor (i.e. model) is the range in actual cone production used in constructing the factor, compared to the possible range of cone production possible in the focal species. During the 17 years (1933-1953) of the Fowells & Schubert (1956) study, the range of cone production documented on 100 ponderosa pine trees was 0 to 338 cones per tree, although a single ponderosa pine can produce up to 12300 cones (Linhart 1988). Similarly for loblolly

pine, the maximum actual total cones included in calculating the conversion factor was 345 in Wasser & Dierauf (1979), and approximately 400 in Wenger (1953), however, this species can produce upwards of 1300 cones per tree (Wasser & Dierauf 1979). The relatively low number of actual cones relative to the number of cones individual trees produce may explain why these conversion factors are linear in form. Or, perhaps the range of cone production considered was not large enough for these authors to detect a non-linearity in the cone abundance data. Only the study by Garman (1951) on Douglas fir indicates a non-linearity in the relationship between the cone index and actual total cones (Table 2-1), with a maximum level of actual cone production of 12000 cones used in the graphical form of this conversion. This conversion is the only one that also reflects the increased difficulty of counting cones as the cone number increases and that the relationship is no longer linear. My derivation encompassed the upper range of cones that individual white spruce trees may produce in good years (8000 to 12000 cones; Nienstaedt & Zasada 1990).

The difference in my mean cone conversion ratio (3.35) and those of other studies outlined, and the non-linear increase in untransformed actual total cones with an increase in visible cones may have important implications for previous studies of white spruce cone and seed production. Studies of conifer masts using a visual cone index without the nonlinear conversion factor might minimise the real variation in the spatial or temporal trend compared to seed counts. The coefficient of variation (CV) for the cone index data ($n = 60$) was 1.28, lower that that for total cones at 1.94. There was no difference in the CV for log-transformed cone index and total cones, with both equal to 1.33. The use of a linear conversion, when a nonlinear conversion better describes the relationship between

the cone index and actual total cones, could affect the structure of the model used to explain patterns of cone and seed production in white spruce (e.g. Greene et *al.* 2002, Calogeropoulos et *al.* 2003), and other species. However, the number of seeds per cone varies among trees and regions (Nienstaedt & Zasada 1990); this variation was not investigated in this study and still deserves attention. Studies using a simple linear conversion (e.g. Wenger 1953, Franklin 1968) underestimate the actual abundance of cones, at least for white spruce. This may also be the case for other conifer species (e.g. Douglas fir and Engelmann spruce) that have a growth form similar to white spruce, and dissimilar to the tree species (mostly *Pinus*) on which current conversion factors in the literature have been based. I suggest that my conversion factor may perform better for these species rather than the conversion factor created for *Pinus* spp., until species-specific conversion factors can be created. I also suggest that this method can likely perform well across the range of white spruce, based on the strong relationship (R^2 of 0.94) between the index and total cones from the Alberta and Yukon sites.

In developing an index it is assumed that detection probabilities are constant across observers, environmental condition, and individuals of the species of interest (Anderson 2001). I suggest that in using the method outlined here that experienced observers conduct cone index estimates on sunny days with the sun behind them and on trees where the area of the crown with cones is clearly visible. Under these conditions variation should be minimised in the detection probability for generating the index. This method will work best when cones are in the top 1/3 of the crown, and used somewhat cautiously when cones are below this. As illustrated with the tree having ~18000 cones (Figure 2-2d) the cones extended to the lowest branches (S. Peters, personal

communication); consequently cone abundance was under-predicted, because more of a tree is unseen as cones move down the crown, proportionally fewer cones are recorded in the index. In other words, the probability of detection of a cone changed. But, if cones are present within the top 1/3 of the crown even at high cone abundance (e.g. the tree with ~6400 cones in Figure 2-2b; S. Peters, personal communication), the log-log conversion model is a reasonable predictor of the actual number of cones.

Variation in cone production is a significant factor in white spruce regeneration and population dynamics of seed predators. Although there are a number of potential limiting factors to white spruce regeneration (e.g., seed viability, seed predation, seedbed availability, etc.), the ability to more accurately assess cone crops (and hence seed production) will provide silviculturalists with a better understanding of tree productivity, and ecologists with improved explanatory abilities in studies of seed predators.

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Table 2-1: Published conversion values for total cone crop estimation from cone index methods. "y" = the actual total number of cones on a tree after felling (unless otherwise indicated), and "x" = the binocular count of all cones from one side of the tree. Other parameters used are indicated. "None" indicates that the conversion factor was determined based solely on assumptions about the crown shape and openness, or the size and/or position of cones in the crown.

Species	Conversion	Sample size	Maximum actual cone value in analysis	Reference
Sugar pine, Ponderosa pine, White fir	y = 1.5x	none	n/a	Fowells & Schubert 1956
Noble fir, Shasta red fir, Western white pine	y = 1.5x	none	n/a	Franklin 1968
Engelmann spruce	y = 2.0x	none	n/a	Franklin 1968
Loblolly pine	y = 2.0x + c*	~ 20	~ 400	Wenger 1953
Loblolly pine	y = 3.02x	36	345	Wasser & Dierauf 1979
Slash pine	y = 2-244x	not reported	not reported	Hoekstra 1960
Slash pine	y = -4.98 + 0.98(2x)	100	~ 620	Webb & Hunt 1965
Douglas fir	Non-linear graph (range 1.5 to 5.3)	11	12,000	Garman 1951

* c is the correction factor for individual observers

Table 2-2: AIC_c comparisons of predictions based on an independent test data set of total cones produced from a range of cone conversion factors found in the literature (Total cones = Cone index · 1.5, Total cones = Cone index · 2.0), the average ratio of index to actual cones based on my data set (3.35), and the conversion presented here (log(Total cones) = 0.073 + 1.189 · log(Cone index)). Akaike weights (w_i) are probabilities that model 'i' is the best fit of the candidate models and only for the data upon which they are evaluated and range from 0 to 1 (Burnham & Anderson 1998). Bold shows the model with the highest w_i value.

	Conversion factor			
	Cone index ·			
	†1.5	‡2.0	3.35	0.073 + 1.189 · log(Cone index)
Model data-set (n = 40 trees)				
log-transformation: AICc	35.74	14.94	-3.57	**-11.71**
ΔAICc	44.41	23.61	5.10	0.00
w_i	<0.01	<0.01	0.02	0.98
Back-transformed: AICc	374.57	370.27	360.78	**356.04**
ΔAICc	18.53	14.23	4.74	0.00
w_i	<0.01	0.01	0.09	0.91
Test data-set (n = 20 trees)				
log-transformation: AICc	21.39	10.64	0.44	**-8.67**
ΔAICc	30.06	19.31	9.11	0.00
w_i	<0.01	<0.01	0.01	0.99
Back-transformed: AICc	389.72	386.91	378.66	**371.09**
ΔAICc	18.63	15.82	7.57	0.00
w_i	<0.01	<0.01	0.02	0.98

†Fowells and Schubert (1956) ‡Wenger (1953), Franklin (1968)

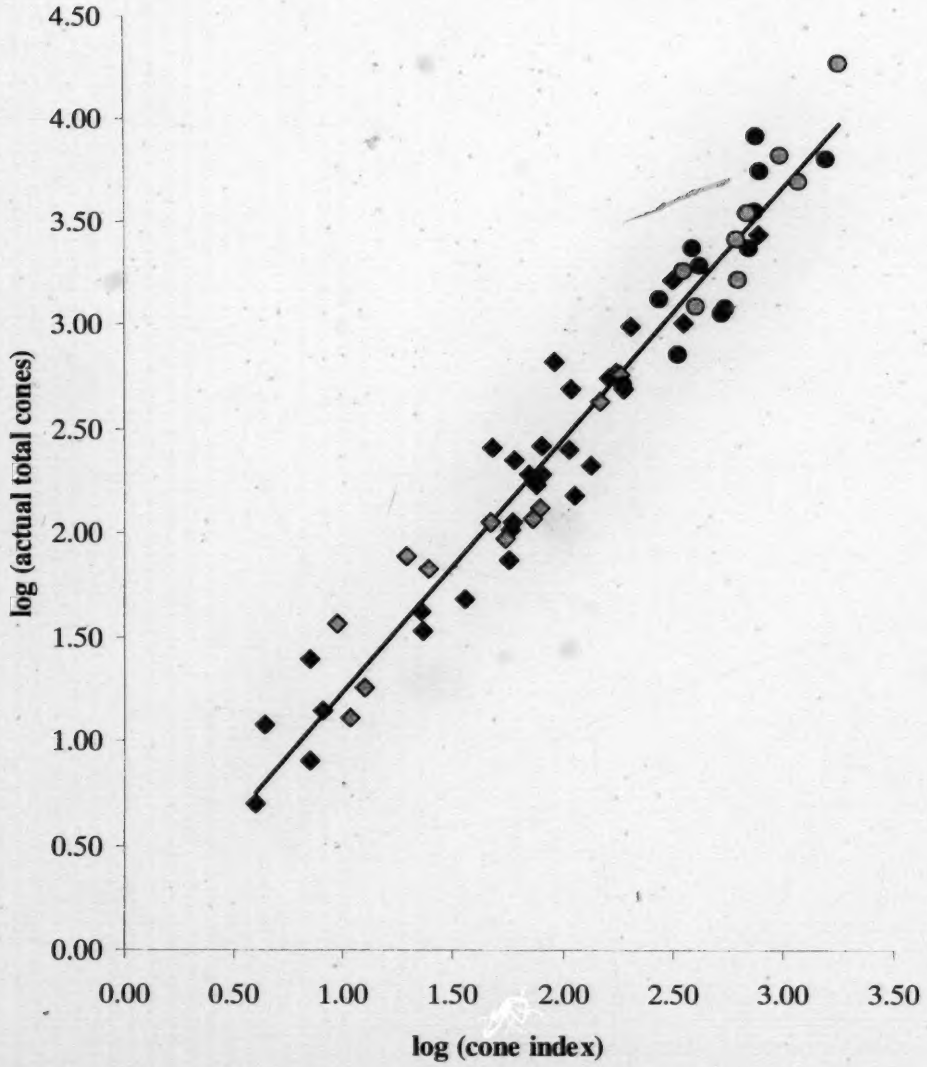

Figure 2-1: The model data set (n = 40, black symbols) and test data set (n =20, grey symbols) for the white spruce cone calibration, showing the relationship between log(cone index) and log(actual total cones) for trees used in regression analysis. Diamonds represent data collected in the Yukon (2002, 2003, 2004) and the Alberta data (1999; Peters et *al.* 2003) data by circles. The regression line is the fit of the log-log conversion created here to the model data set, y = 0.073 + 1.189x (R^2 = 0.94).

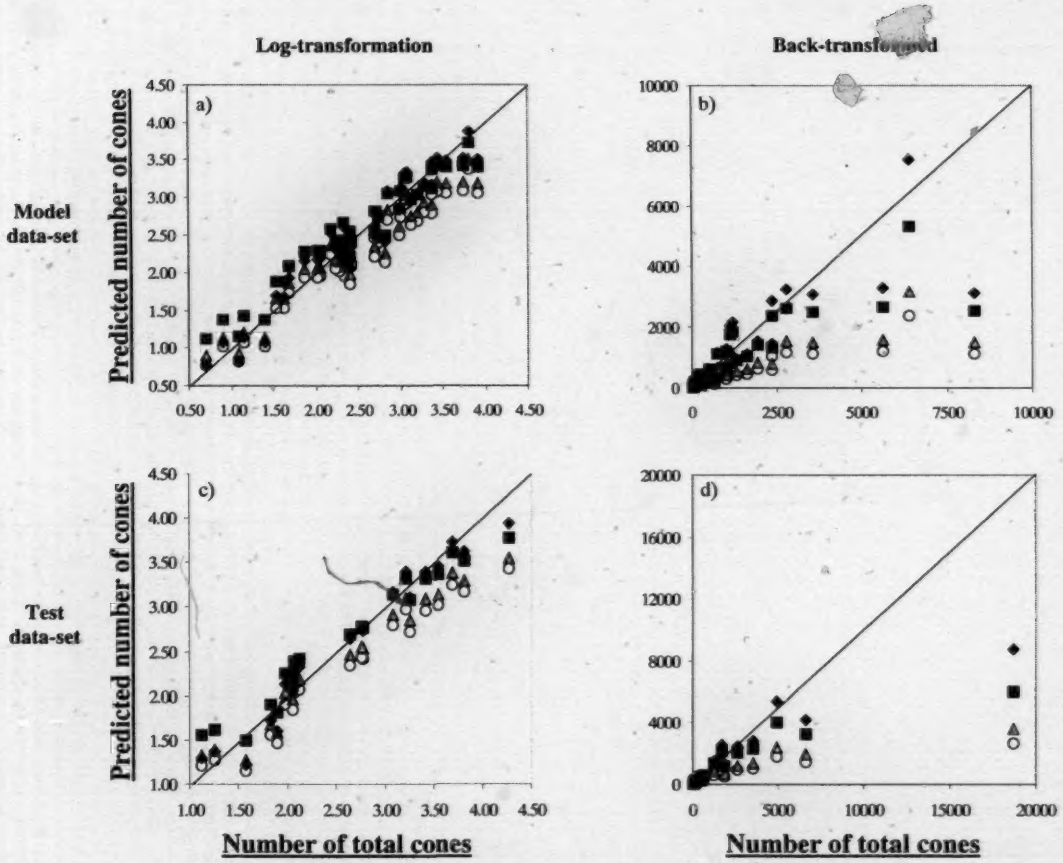

Figure 2-2: Observed and predicted actual total cones from each the four models in Table 2-2 (open circles represent predictions based on: cone index · 1.5, triangles: cone index · 2.0, squares: cone index · 3.35, and black diamonds: 0.073 + 1.189 · log(cone index)). Panels 'a' and 'b' show the fits of the model data set for log-transformed and back-transformed data, respectively, and panels 'c' and 'd' show the fits for the test data set. The 1:1 line represents that observed and predicted cone abundances are equal (a perfect model). Note that the scale of the axes varies among panels.

CHAPTER 3

DELINEATING MAST-SEEDING YEARS ACROSS SPECIES AND STUDIES: A GENERAL METHOD

INTRODUCTION

The intermittent production of large seed crops by a plant population, known as mast seeding (Kelly 1994) is widely studied. Mast seeding is of interest for its effects on plant population regeneration, as a resource pulse for higher trophic levels, and from an evolutionary perspective (e.g., Janzen 1971, Silvertown 1980, Kelly et *al.* 1994, Jones et *al.* 1998, Ostfeld & Keesing 2000, Kon et *al.* 2005). Mast seeding occurs in many plant species, and is the most well known example of a resource pulse for seed consumers; when resources temporarily occur at much higher levels than normal (Ostfeld & Keesing 2000). The occurrence of mast seeding by a plant population is identified by the temporal variability of seed production based on the coefficient of variation (CV = SD / mean), with plant populations exhibiting mast seeding behaviour having a CV > 1 (Kelly 1994, Liebhold et *al.* 2004). Although this quantitative criterion can be used across species, there is no such criterion for identifying "mast years" (Herrera et *al.* 1998). This is a necessary first step to investigate patterns in the frequency and magnitude of mast seed years within and between species. A standard technique will also benefit future meta-analyses to synthesize mast seeding and resource pulse literature that could otherwise be confounded by different methods for delineating these mast years.

Mast years can be difficult to identify because very few species show 'strict masting' where either no seeds or many seeds are produced in a year; rather in masting species seed production can be near continuous (Kelly 1994). In the literature, mast-seed

years have been identified by seed production above some value (McShea 2000) and qualitatively as "good" years when most trees produced seed and seeds exist in their entire crown (Suzuki et *al.* 2005). In general, these methods fail to account for variability in seed production potential between species, or sites with different biotic and abiotic conditions that influence seed output (Greene et *al.* 2002).

Here I reviewed some potential methods to quantitatively define a mast year, and I suggest a simple method for objectively quantifying mast years. In doing so, I examined a variety of plant species and a variety of sampling techniques used to measure seed production. My intent was to capture the qualitative descriptions of the quantity of seed produced within mast years. The literature suggests quite clearly that seed production in mast years are well above average for the population and species of interest, being described as: large (Piovesan & Adams 2001), unusually large (Taylor & Aarssen 1989), high (Kelly & Sork 2002), vast (Silvertown 1987), mass (Ruscoe et *al.* 2005), and huge (Allen & Platt 1990). Or, that in mast years heavy seed crop is produced, while in other years there is no, poor, or only moderate seed production (Norton & Kelly 1988). Based on these descriptions of seed production during a mast year, "mast years" could be quantitatively defined as: 1) years with seed production greater than some set value (e.g., McShea 2000), 2) large seed production years that create CV >1 or positive skew in the data set (explored here), 3) years with seed production greater than the mean (e.g., Curran et *al.* 1999), or 4) years with seed production greater than the mean by a designated amount based on the variability in seed production around the long-term mean (this study). I investigated each of these approaches using 36 data sets from the literature covering a variety of plant species.

METHODS

DATA SETS

I found 36 time series in the literature on annual mean seed production that demonstrated mast seeding (CV>1). Annual seed production was obtained directly from tables or digitized from figures (Table 3-1, Figure 3-1 left column). The four *Picea glauca* data sets were from the mean annual cone production of 50 to 86 trees per site in Yukon, Canada (see Chapter 5 for methods). I included only data-sets with a minimum time series length of 10 years (max. 37 years, mean = 18.8 years) to obtain variability in seed output over time, and that presented untransformed data. Data sets included a variety of species, deciduous and coniferous trees, grasses, and legumes, and a variety of sampling techniques (e.g., seed traps, acorn or cone counts on trees or in sampling buckets, inflorescences per plant). I used data represented as yearly means based on the number of seeds (or its surrogate) per plant or a measure of seed density. If data were presented as one species in multiple sites, each site was used and where a common site with multiple species was presented, each species was used.

DELINEATION OF MAST YEARS

As mentioned previously, based on qualitative suggestions that during a mast-seeding year the quantity of seed produced is very large, "mast years" could be quantitatively defined as:

1. years with seed production greater than some set value (e.g., McShea 2000),
2. years that through stepwise removals of the highest seed production years ("mast years") to i) reduce the CV to ≤ 1, or ii) remove positive skew in the

data set (explored here),

3. years with seed production greater than the mean (e.g., Curran et *al.* 1999), or
4. years with seed production greater than the mean by a designated amount based on standardized deviates (this study).

While these methods are largely self-explanatory, I describe them further in the following section. Briefly, for the standardized deviate method (method 4) I first suggest that annual seed production be expressed as a standardized deviate based on the long-term average seed production and variability of the sampled population:

$$\text{Annual deviate from the long-term mean}_i = \frac{\text{mean seed production}_i \text{ in year 't'} - \text{long-term mean seed production}_i}{\text{standard deviation calculated over all years}_i}$$

This quantifies for site 'i' (the sampling area) the number of standard deviations from the long-term mean seed production is in year 't'. Years when seed production is near the overall mean abundance will be close to 0 standard deviates from the mean, years when seed is less than the mean will have a negative standard deviate, and "mast years" will have a relatively high positive standard deviate. Cut-off values for identifying mast years are discussed below. Like the CV, the annual standardized deviate is unitless, allowing for comparisons between species, sites varying in productivity, and sampling techniques.

The general applicability of each of these quantitative definitions were assessed on the basis of their rationale and directly applied to each of the data sets. The robustness of the results from these methods was compared to the literature on seeding patterns. This included that sites might differ in their quality and be reflected in the magnitude of seed produced (Greene et *al.* 2002), and that consecutive high seed production years are

rare (Greene & Johnson 2004). In addition, I tested for the effects of vegetation type and type of data collected (see Table 3-1) on the proportion of years in a dataset that were identified as mast years using analysis of variance.

RESULTS & DISCUSSION

Across all data sets, the variability in seed production ranged from a low CV of 1.15 to a high of 3.30 (Table 3-1), and included the highest CV values published. Eight species were represented at least twice in the data-sets, with variation in their CV among sites. The most extreme variation was seen in *P. glauca*, ranging from a CV of 1.30 to 2.71.

Most of the methods tested did not prove promising for being either biologically or mathematically conducive for general applicability. The first method, years with seed production greater than some designated value, fails to account for variability in overall productivity between sites (Greene et *al.* 2002), and provides no criteria for setting the designated value. For example, McShea (2000) defined a mast crop year as when seed output was above 300kg $\cdot$ ha^{-1} of acorns. However, across the study area, long-term site means ranged from 34.4 to 243.3 kg acorns $\cdot$ ha^{-1} (McShea 2000). At the low end of productivity, although a site was undergoing mast seeding (CV>1), no mast years were detected using this 'set-value' approach.

Mast seeding populations generally have a right-skewed distribution of seed production across years (Greene & Johnson 2004), with fewer large seed production years and many lower seed production years. Stepwise removals of the large seed years might be a way to identify mast years, as those years that result in removing significant right-skew or reducing the CV to <1 (method 2). I found that the CV was not

consistently reduced with sequential removal of the ranked seed production years. Only one-third of the data sets showed a CV reduction to <1, and all displayed some subsequent increase in CV with subsequent large seed years removed. In most instances the CV actually increased with stepwise removals, since the mean was reduced only slightly and the SD remained high (analyses not shown). Similar problems arose when I attempted to reduce skew. After systematic removals of each of the top 10 seed production years, only seven of the 36 data sets transitioned from significant skew to no significant skew. The transition occurred after one to four top seed production years were removed, and the result was consistent with subsequent removals. Another 11 data sets fluctuated in showing significant skew with the removal of high-seed years; and after 10 years, seven data sets were either not long enough, or had any variation left with which to allow calculations for skew to be conducted. The remaining 11 data sets did not show a deviation from being significantly skewed after the top 10 seed production years were removed. This suggested that over 50% of years could be mast years (mean time series length = 18.8 years), and was unlikely. Overall, the response of the data sets to systematic removals of high seed years were very sensitive to the remaining data and did not display the consistency required for these stepwise removal to be a viable method for identifying mast seeding years.

Mast seeding years could also be identified based on when the annual seed production is greater than the long-term mean (method 3). Since mast-seeding populations are generally right-skewed (Greene & Johnson 2004) the arithmetic mean is greater than the median, limiting the number of potential mast years to less than half of the time series. This criterion has rarely been implemented in the literature (Curran et *al.*

1999, see Koenig & Knops 2001 for a similar criteria). If this criterion were used here, 27% ± 1% (mean ± SE) of years would be mast years. Further, 25% of the data sets would show at least one, and up to four sets of consecutive mast years. Consecutive years with very high seed production are considered highly unusual (Greene & Johnson 2004). In most of these cases seed production was only slightly above the long-term mean, and suggested that this definition of mast years may be too liberal. This also suggested that an objective method is needed to determine how much seed production should be above average to qualify as a mast (method 4). In addition, seed production is frequently more continuous than just high and low seed years (Kelly 1994; Figure 3-1, centre column), and often the mean fell within the range of continuous seed production (e.g., Figures 3-1a, 3-1i, 3-1m, 3-1t, 3-1z, 3-1ad; But see 3-1u, 3-1ae, 3-1aj).

Maximum annual standard deviates from the mean were most often in the range of two to three, and rarely greater than four (Figure 3-1). The minimum was as low as –0.9, and increased with the CV of the population (Figure 3-2). Thus, plant populations with high CVs had much higher deviations in seed production above the long-term mean, compared to below. In strongly mast-seeding populations (CVs >> 1) the long-term mean was relatively low due to many years with no seed, and the large CV was driven by a few years with relatively high seed. As a result there was lower variability below the long-term mean (small negative standard deviates). This is in contrast to populations with lower CVs (weaker mast-seeding populations) that tended to have a relatively higher mean with greater variation below it. I suggest using this pattern to designate mast years as those years when the standardized deviate is greater than the absolute magnitude of the minimum variation below the long-term mean. This creates, regardless of plant

population CV, an equal range of possible deviations on either side of the mean that are not mast years.

The number of mast seed years delineated by the standardized deviate method (method 4) ranged from one to six (Figure 3-1, solid bars). On average 17% ± 1% of years were identified as mast years. There was no significant influence of vegetation type (coniferous, deciduous, legume, or tussock; $F_{0.05, 3, 32} = 0.230$, $P = 0.876$), or type of data collected (e.g., seeds · m^{-2}, cones · $tree^{-1}$, see Table 3-1; $F_{0.05, 7, 28} = 0.370$, $P = 0.913$) on the arc-sine square-root transformed proportion of years identified as mast years. In only one case were two consecutive years delineated as mast seeding years (Figure 3-1i), and on average over all data sets, the inter-mast interval was 5.25 ± 0.71 years. In relation to the expectations of mast seeding (i.e. years of very large seed crops, non-consecutive mast years), this method performed well. I also explored how changing the cut-off for standard deviates above the long-term mean affected the results. For instance, if the absolute value of the *average* deviation below the mean was used, the value of cut-offs and resulting mast year delineations changed very little (to 18% ± 1% of years). This was due to the multiple years of low seed production in the data sets and the magnitude of deviations above the mean. Thus, it appeared that the number of mast years identified in the data sets was relatively insensitive to this criterion.

The standardized deviate method is an objective quantitative method for identifying mast years that allows for consistent description of mast seeding patterns across species and populations. This fills a gap in the mast seeding literature that has been surprisingly vague on this topic. For instance, all studies included here used empirical data, and most discuss mast years and their cause or consequences; but few

defined what constituted a mast seed year for their data (McShea 2000, Suzuki et *al.* 2005). This method builds on Herrera et *al.* (1998) and Kelly et *al.* (2000) who standardized time series data in the manner suggested above but they did so after log-transforming the data. Log-transforming seed production normalizes the distribution and removes skew (Norton & Kelly 1988, Koenig et *al.* 1994). But, as suggested Norton & Kelly (1988), the resulting normal distribution provided no objective point with which to identify mast years. I used the distribution of the raw data to identify mast-seeding years, whereby the population has many more years of low seed production with intermittent high seed 'mast' years.

Here I provide a method to delineate mast years, however, non-mast years are a different issue. For populations exhibiting seed crop failures, I suggest that years in which the seed crop is zero, in other words years with no seeds for plant recruitment or food for seed predators be grouped together. The years that fall between a zero year and a mast year may be grouped into one or more classes based on the standardized deviates to categorize all years prior to analysis. Or, the standard deviates could be applied in regression-type analyses to synthesize general patterns of the response of seed predators or seedling recruitment levels to continuous variation in seed output. In either case, I suggest future studies should work towards integrating the knowledge in the literature on mast seeding and resource pulses in meta-analyses using the consistent, quantitative method presented here. I hope that the method shown will promote cross-study comparisons and integration of mast seeding studies across species to help elucidate generalities for proximate and ultimate causes of mast seeding and its consequences. This study also indicated that the proportion of years classified as mast years is relatively

similar across species, and is an area for further investigation.

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Table 3-1: Data-sets used in analyses of mast years, ranked by increasing values of CV among years. Letters after species names represent different sites within a study. 'n' is the number of years of seed production data, 'Data' is the type of seed data collected (see footnote), 'Mean' refers to the mean number of seed produced in the data-set (see 'Data' for units of seed production), 'SD' is the standard deviation of seed production over time, 'CV' is the coefficient of variation of seed production among years.

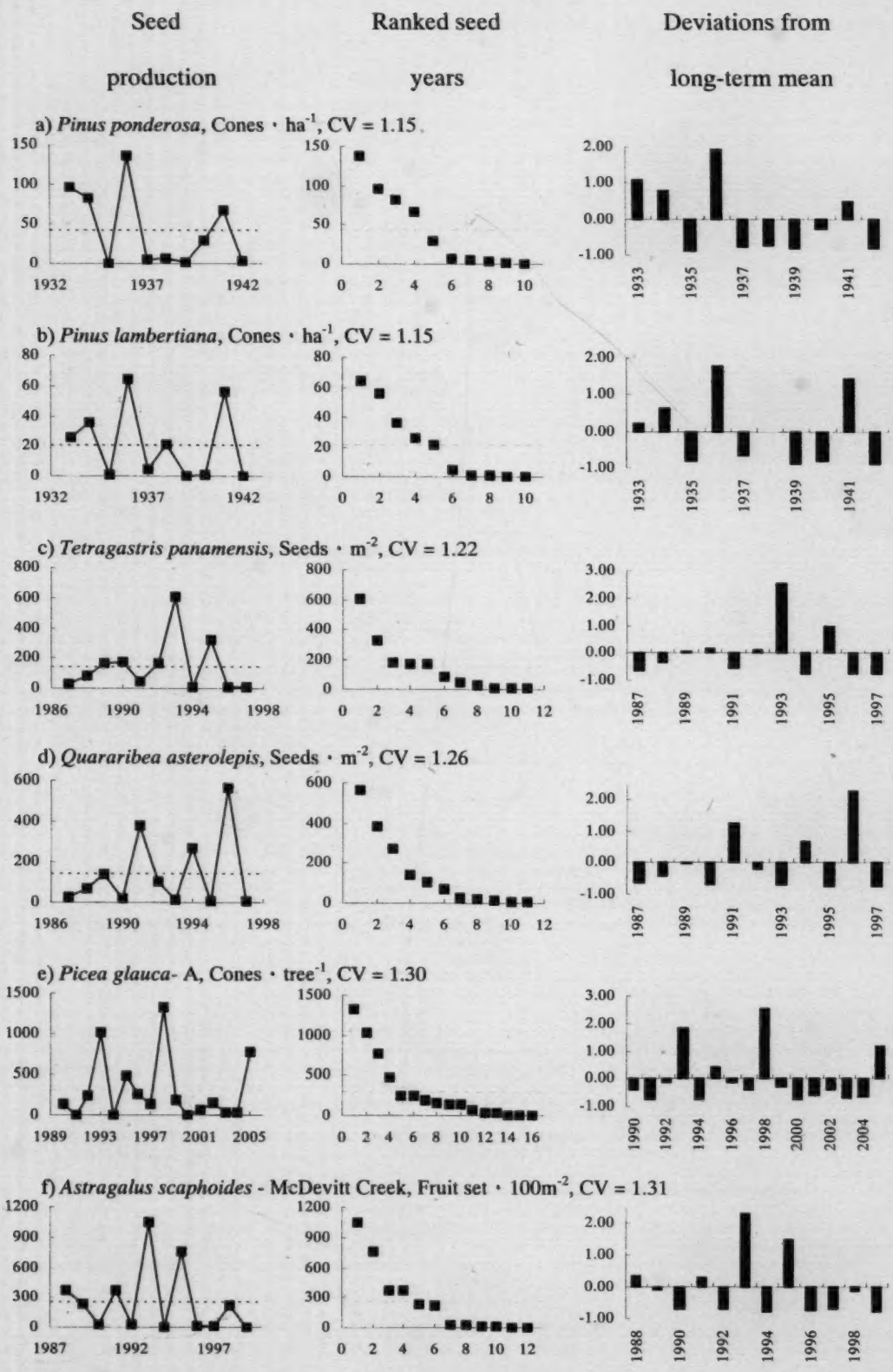
ID	Species	n	Data	Mean	SD	CV	Source
1a	*Pinus ponderosa*	10	5	42.8	49.2	1.15	Fowells & Schubert 1956
1b	*Pinus lambertiana*	10	5	21.0	24.2	1.15	Fowells & Schubert 1956
1c	*Tetragastris*	11	1	148.4	181.4	1.22	DeSteven & Wright 2002
1d	*Quararibea*	11	1	146.6	184.6	1.26	DeSteven and Wright 2002
1e	*Picea glauca*- A	16	3	304.3	396.2	1.30	LaMontagne & Boutin
1f	*Astragalus scaphoides* – McDevitt Creek	12	4	258.1	338.2	1.31	Crone & Lesica 2004
1g	*Quercus rubra*	11	2	13.5	17.9	1.32	Healy et *al.* 1999
1h	*Pinus monticola*	21	3	21.6	28.6	1.33	Eis 1976
1i	*Dacrydium cumpressinum*	33	1	312.7	421.6	1.35	Norton & Kelly 1988
1j	*Picea glauca*- B	16	3	164.3	231.5	1.41	LaMontagne & Boutin
1k	*Pseudotsuga menziesii*	37	3	494.6	709.2	1.43	Eis 1973

1l	*Fagus crenata*- Kanumazawa	11	1v	80.6	119.5	1.48	Suzuki et *al.* 2005
1m	*Chionochloa oreophila*†- CC	19	6	0.646	1.005	1.55	Kelly et *al.* 2000
1n	*Astragalus scaphoides* - Haynes	14	4	120.4	187.7	1.56	Crone & Lesica 2004
1o	*Quercus* spp. - Bear	12	7	125.6	202.1	1.61	McShea 2000
1p	*Chionochloa conspicua*†- CC	19	6	6.762	10.987	1.63	Kelly et *al.* 2000
1q	*Picea glauca*- C	15	3	184.1	302.7	1.64	LaMontagne & Boutin
1r	*Pinus ponderosa*	24	1v	0.648	1.079	1.66	McDonald 1992
1s	*Chionochloa pallens*†- TV	26	6	1.447	2.405	1.66	Kelly et *al.* 2000
1t	*Abies grandis*	37	3	92.1	153.7	1.67	Eis 1973
1u	*Abies concolor*	10	5	50.5	86.7	1.72	Fowells & Schubert 1956
1v	*Chionochloa rubra*†- TV	26	6	2.132	3.668	1.72	Kelly et *al.* 2000
1w	*Chionochloa flavescens*†- CC	20	6	0.766	1.356	1.77	Kelly et *al.* 2000
1x	*Chionochloa pallens*†- MH	13	6	7.951	14.282	1.80	Kelly et *al.* 2000
1y	*Chionochloa crassiuscula*†- CC	19	6	1.314	2.433	1.85	Kelly et *al.* 2000
1z	*Chionochloa pallens*†- CC	19	6	2.079	3.850	1.85	Kelly et *al.* 2000
1aa	*Fagus crenata*- Appi	12	1v	109.9	208.8	1.90	Suzuki et *al.* 2005

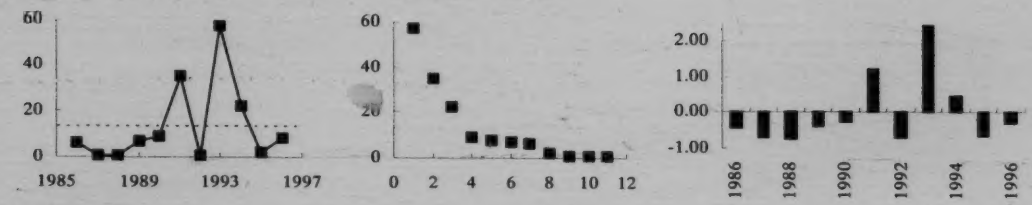
1ab	*Chionochloa rubra*[†]- CC	19	6	3.761	7.364	1.96	Kelly et *al.* 2000
1ac	*Fagus crenata*- Hayasaka	12	1v	44.6	96.2	2.16	Suzuki et *al.* 2005
1ad	*Chionochloa rigida*[†]- TV	26	6	1.508	3.355	2.23	Kelly et *al.* 2000
1ae	*Abies concolor*	24	1v	0.380	0.846	2.23	McDonald 1992
1af	*Pseudotsuga menziesii*	24	1v	0.426	0.966	2.27	McDonald 1992
1ag	*Chionochloa teretifolia*[†]- TV	26	6	2.827	7.411	2.62	Kelly et *al.* 2000
1ah	*Picea glauca*- D	13	3	342.0	927.8	2.71	LaMontagne & Boutin
1ai	*Chionochloa crassiuscula*[†]- TV	26	6	0.365	1.124	3.08	Kelly et *al.* 2000
1aj	*Calocedrus decurrens*	24	1v	0.046	0.152	3.30	McDonald 1992

1) seeds·m^{-2}, 1v) viable seeds·m^{-2}, 2) acorns·m^{-2}·$tree^{-1}$, 3) cones·$tree^{-1}$, 4) fruit set·$100m^{-2}$, 5) cones·ha^{-1}, 6) Inflorescenses per plant, 7) acorns(kg)·ha^{-1}

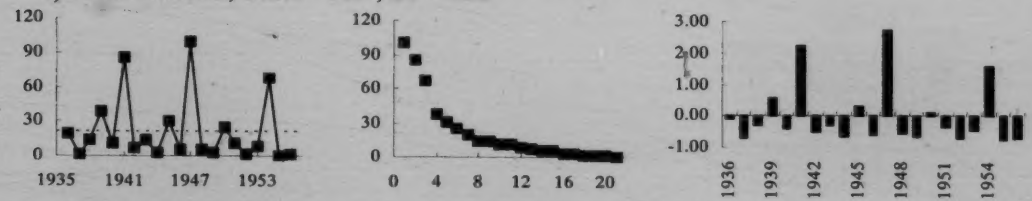
[†] Different significant digits used for these data sets due to the scale of measurement used


Seed production
Ranked seed years
Deviations from long-term mean
a) Pinus ponderosa, Cones · ha-1, CV = 1.15
b) Pinus lambertiana, Cones · ha-1, CV = 1.15
c) Tetragastris panamensis, Seeds · m-2, CV = 1.22
d) Quararibea asterolepis, Seeds · m-2, CV = 1.26
e) Picea glauca- A, Cones · tree-1, CV = 1.30
f) Astragalus scaphoides - McDevitt Creek, Fruit set · 100m-2, CV = 1.31

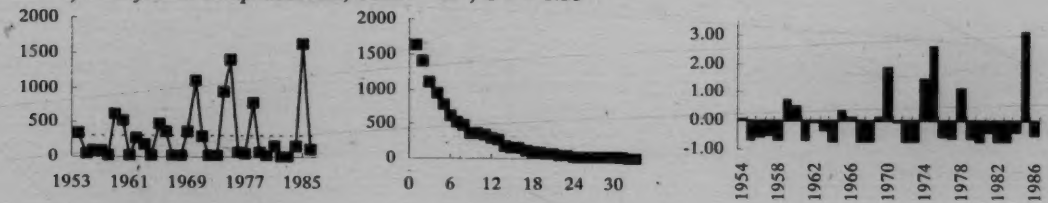
g) *Quercus rubra*, Acorns · m^{-2} · $tree^{-1}$, CV = 1.32



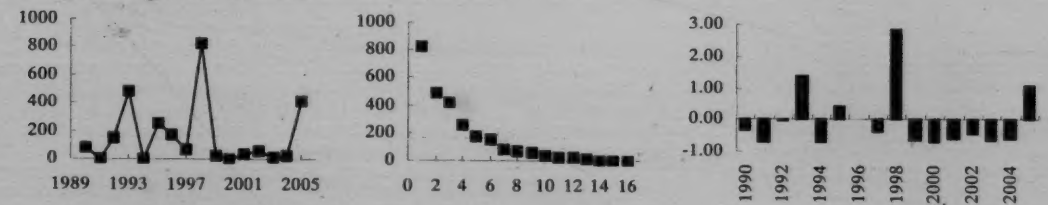
h) *Pinus monticola*, Cones · $tree^{-1}$, CV = 1.33



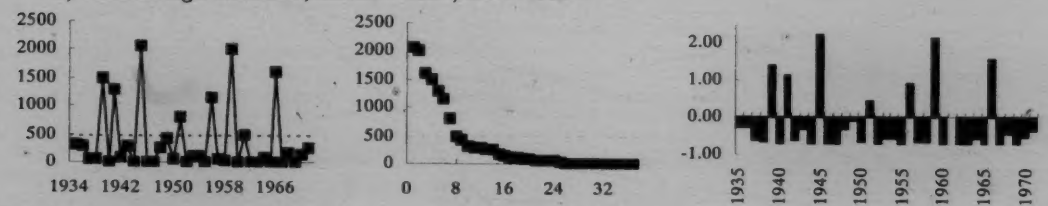
i) *Dacrydium cumpressinum*, Seeds · m^{-2}, CV = 1.35



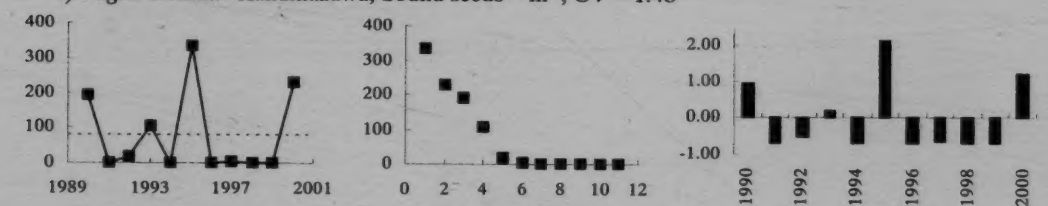
j) *Picea glauca*- B, Cones · $tree^{-1}$, CV = 1.41



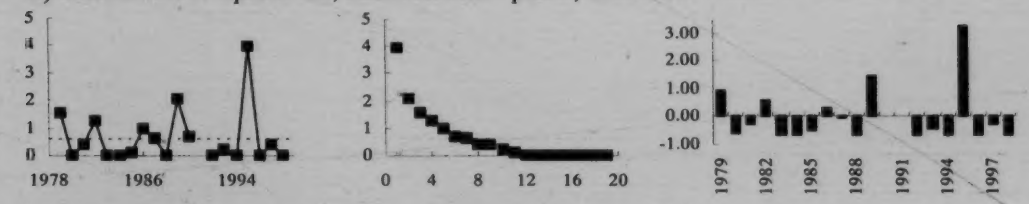
k) *Pseudotsuga menziesii*, Cones · $tree^{-1}$, CV = 1.43



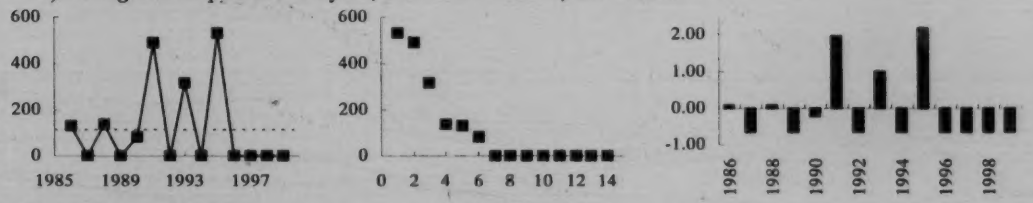
l) *Fagus crenata*- Kanumazawa, Sound seeds · m^{-2}, CV = 1.48



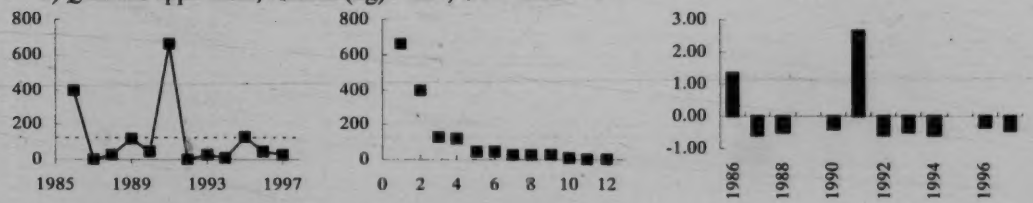
m) *Chionochloa oreophila*- CC, Inflorescences · plant^{-1}, CV = 1.55



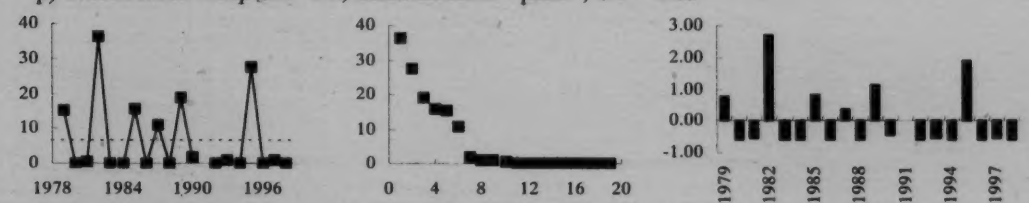
n) *Astragalus scaphoides*- Haynes, Fruit set · 100m^{-2}, CV = 1.56



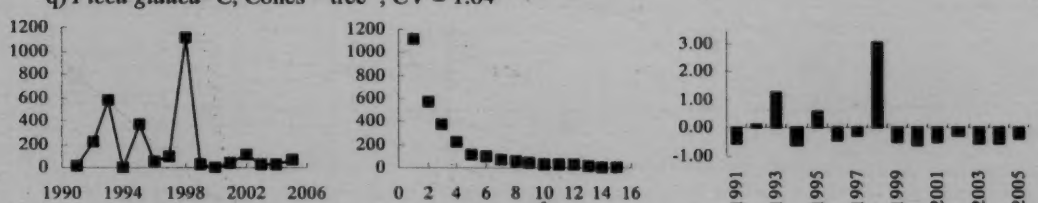
o) *Quercus* spp.- Bear, Acorns (kg) · ha^{-1}, CV = 1.61



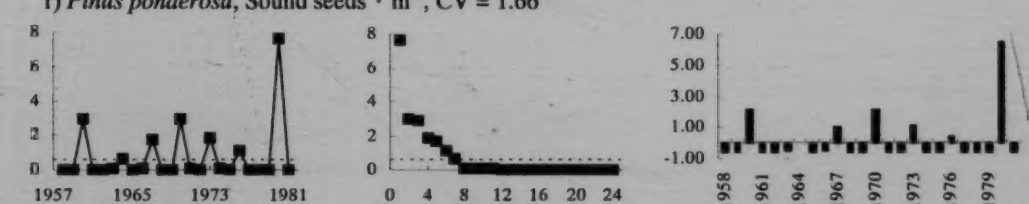
p) *Chionochloa conspicua*- CC, Inflorescences · plant^{-1}, CV = 1.63



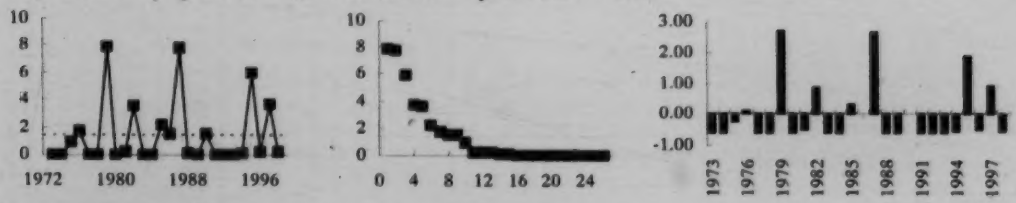
q) *Picea glauca*- C, Cones · tree^{-1}, CV = 1.64



r) *Pinus ponderosa*, Sound seeds · m^{-2}, CV = 1.66

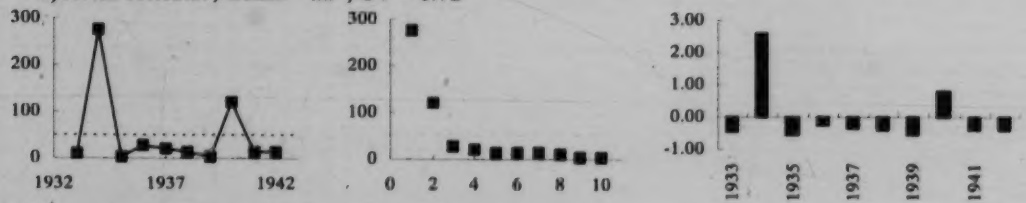


s) *Chionochloa pallens*- TV, Inflorescences · plant^{-1}, CV = 1.66

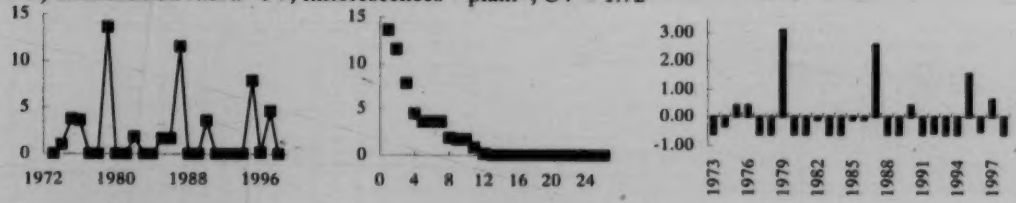


t) *Abies grandis*, Cones · tree^{-1}, CV = 1.67

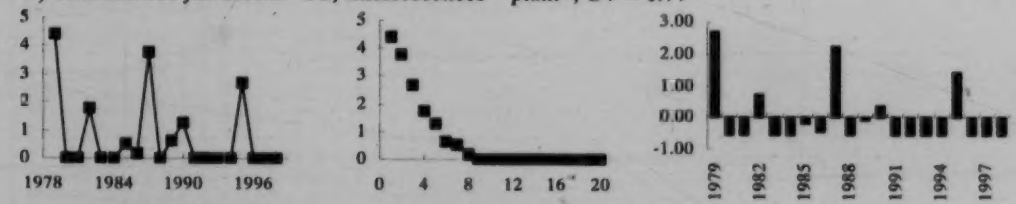
u) *Abies concolor*, Cones · ha^{-1}, CV = 1.72



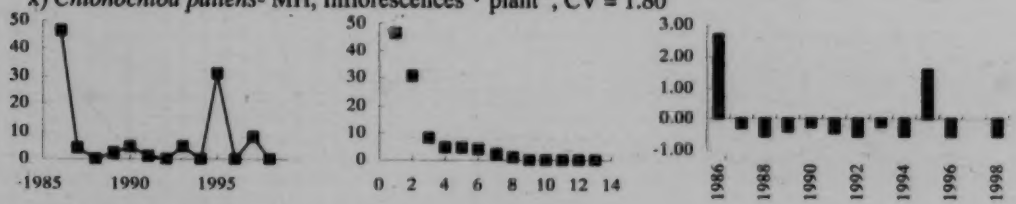
v) *Chionochloa rubra*- TV, Inflorescences · plant^{-1}, CV = 1.72



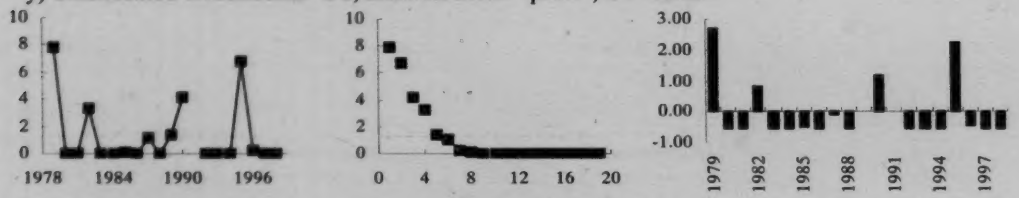
w) *Chionochloa flavescens*- CC, Inflorescences · plant^{-1}, CV = 1.77



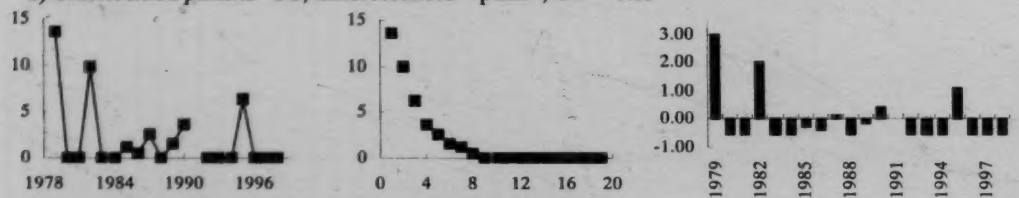
x) *Chionochloa pallens*- MH, Inflorescences · plant^{-1}, CV = 1.80



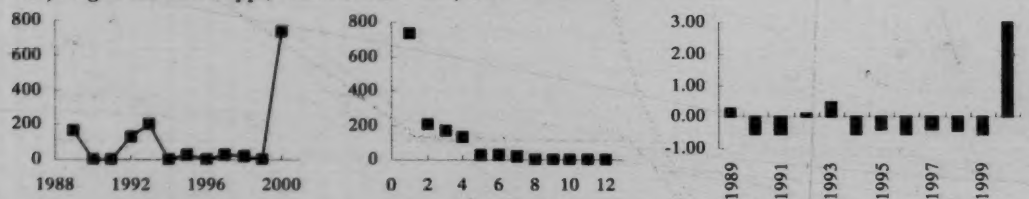
y) *Chionochloa crassiuscula*- CC, inflorescences · plant^{-1}, CV = 1.85



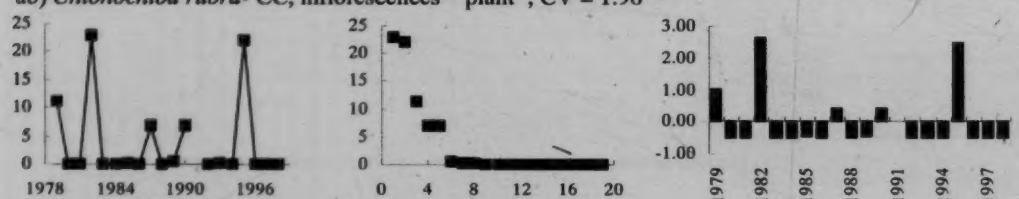
z) *Chionochloa pallens*- CC, inflorescences · plant^{-1}, CV = 1.85



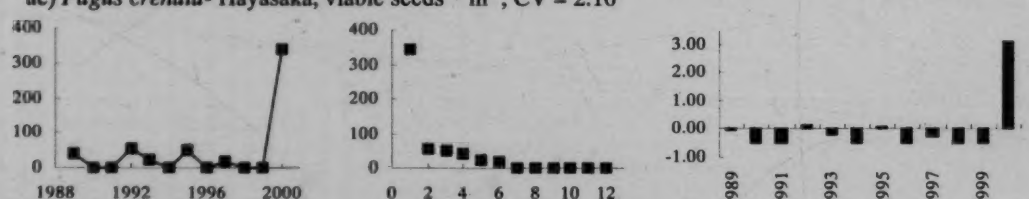
aa) *Fagus crenata*- Appi, viable seeds · m^{-2}, CV = 1.90



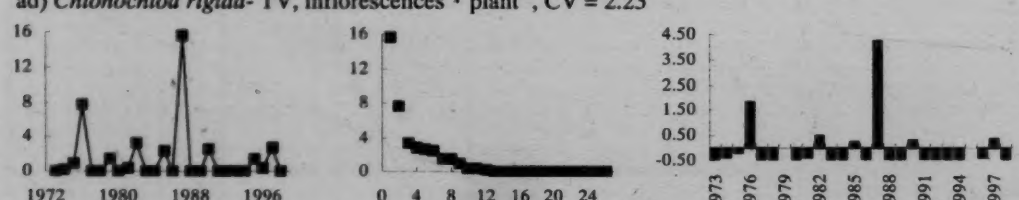
ab) *Chionochloa rubra*- CC, inflorescences · plant^{-1}, CV = 1.96



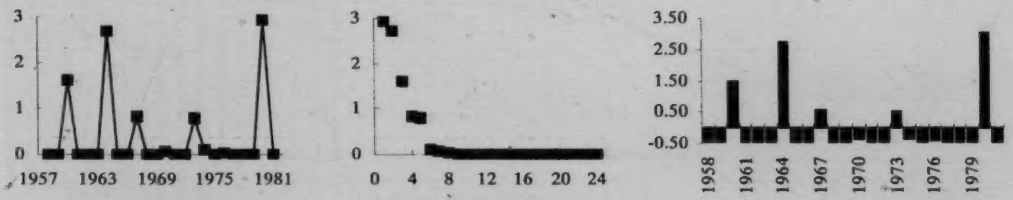
ac) *Fagus crenata*- Hayasaka, viable seeds · m^{-2}, CV = 2.16



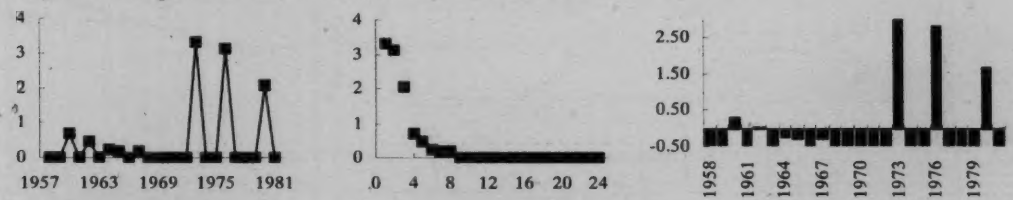
ad) *Chionochloa rigida*- TV, inflorescences · plant^{-1}, CV = 2.23



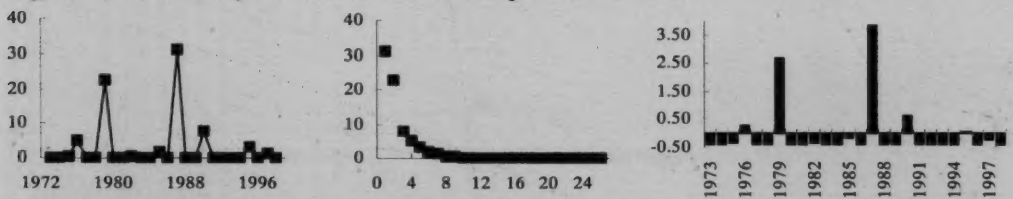
ae) *Abies concolor*, Viable seeds · m^{-2}, CV = 2.23



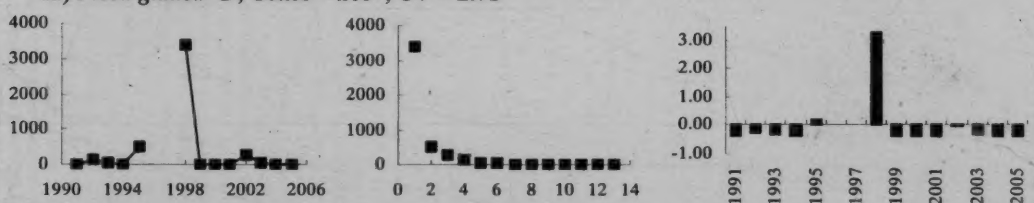
af) *Pseudotsuga menziesii*, Viable seeds · m^{-2}, CV = 2.27



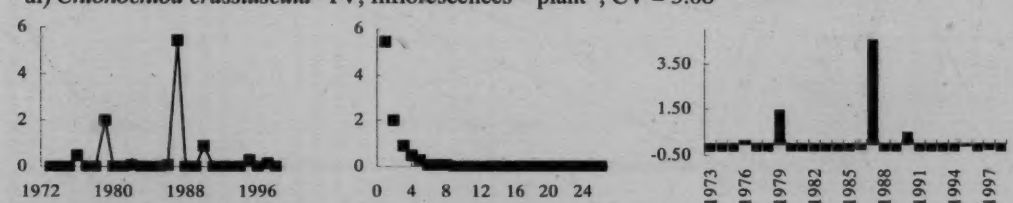
ag) *Chionochloa teretifolia*- TV, Inflorescences · $plant^{-1}$, CV = 2.62



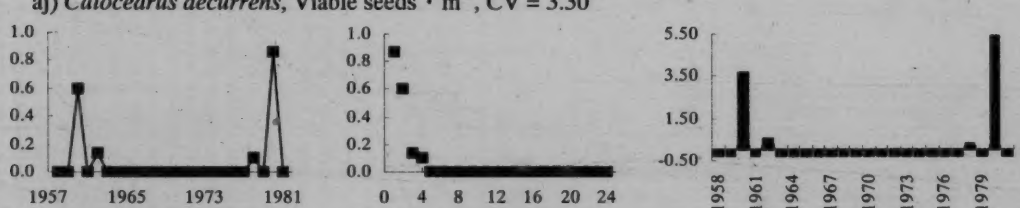
ah) *Picea glauca*- D, Cones · $tree^{-1}$, CV = 2.71



ai) *Chionochloa crassiuscula*- TV, Inflorescences · $plant^{-1}$, CV = 3.08



aj) *Calocedrus decurrens*, Viable seeds · m^{-2}, CV = 3.30



Year Rank Year

Figure 3-1: Measurements of mean annual seed production for 36 data sets (left panel), their ranked distribution of seed (centre panel), and variation in annual means shown as the number of standard deviations from the long-term mean (right panel). Years identified as mast-seeding years based on the standardized deviate method are indicated by solid symbols and bars. Horizontal dashed lines represent the long-term mean seed production across years for each data-set. Data-sets are ordered by increasing CV among years. Note: species, site (if applicable) and CV are indicated in the subheadings. Y-axis variables in the first 2 panels vary and are indicated for each plot; in the centre panel the seed output years are ranked from high to low, rank appears in the x-axis. See Table 3-1 for more information.

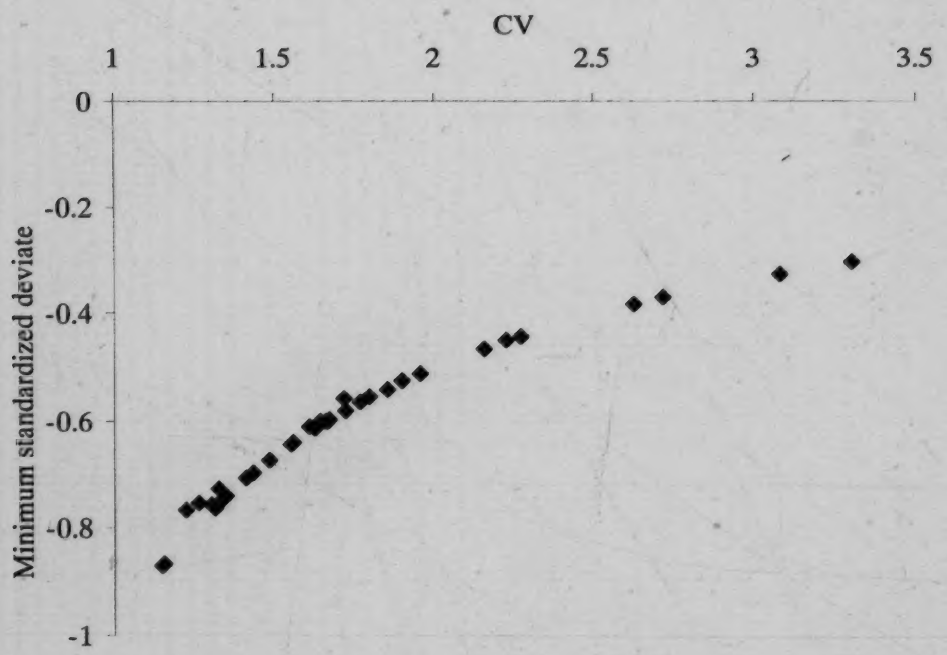


Figure 3-2: The minimum standardized deviate for the 36 seed production data sets increases with increases in CV.

CHAPTER 4

EFFECTS OF FOOD AVAILABILITY AND CONSPECIFIC DENSITY ON RED SQUIRREL (*Tamiasciurus hudsonicus*) POPULATION DYNAMICS

INTRODUCTION

Identifying and understanding the factors that determine population growth rates is a prominent question in ecology. Weather conditions, food supply, population density, predation, and disease have all been reported as significant predictors of population growth patterns (Begon et *al.* 1996). Food abundance often has a major influence on survival and breeding success of individuals (Dobson & Kjelgaard 1985; Boutin 1990; Nagy & Holmes 2005) that in turn affects population growth. Density can affect future population size through negative feedback on demographic rates as population density increases (Turchin 1999). Density dependence has been used to describe the effect of either increased intraspecific competition as density increases through reductions in per capita resources or, unrelated to competition, through increased incidence of predation or disease at higher densities (Begon et *al.* 1996). Furthermore, territorial behaviour can enhance the effect of density through the defence of resources and competition for space (Both & Visser 2003), and has been proposed to have a stabilizing effect on population dynamics (Watson & Moss 1970). When territory size is inflexible, population growth may be prevented through excluding potential recruits when all territories are occupied (Watson & Moss 1970; Rusch & Reeder 1978). However, if territory size is flexible and fluctuates with food or density, variable population growth may result (Adams 2001).

A population dynamics model including only population density is frequently used to describe single-species dynamics, with variation in per capita food availability

inferred from fluctuations in population density (Choquenot 1998; Sibly & Hone 2003); this is largely because it is often very difficult to quantify food availability in nature (Sæther 1997). In these cases, the underlying assumption is that the total amount of food available tends to be relatively constant from year to year. However, temporal variability in the availability of food is more likely, and the effects of fluctuations in food need to be teased out from density effects (Choquenot & Ruscoe 2000). For example, Newton (1998) examined literature on reproduction in birds and found no studies that considered variable food availability when examining the effects of density. Although predator-prey studies deal with variable predator densities and temporally variable prey resources, the dynamics of the consumer and its resource are coupled.

The effects of food and population density on population growth could potentially be decoupled in resource pulse systems. For example, seed production by many plant species is highly temporally variable (Fenner & Thompson 2005; Chapter 3), and its availability may have direct effects on seed-predator populations (Wolff 1996; McShea 2000; Ostfeld & Keesing 2000). Although seed production affects the consumer (seed predator) population, consumer population density would not feedback onto the level of seed production the following year (except perhaps as an evolutionary phenomenon; Kelly 1994). Temporally variable food availability may occur independent of population density; whereas population density could affect per capita resources or act through the availability of other resources, such as space. The factors of food availability and population density may act separately or together to produce observed population dynamics (Karels & Boonstra 2000; Wang et *al.* 2006). When temporal variation in food abundance along with long-term data on consumer population density can be quantified

and they are not coupled, the relative effects of food and density on population growth can be examined.

In this chapter I investigated the separate and combined effects of food availability and population density on North American red squirrel (*Tamiasciurus hudsonicus*) population growth rates in the southwest Yukon, Canada. The presence of a single mast-seeding conifer species, white spruce (*Picea glauca*), whose seeds comprise the majority of the red squirrel diet, causes marked annual variation in food availability (Chapter 3). Red squirrel population fluctuations have previously been related to food availability (C. Smith 1968; Kemp & Keith 1970; Sullivan 1990); however, Rusch & Reeder (1978) found that red squirrels maintain stable population densities. Rusch & Reeder (1978) hypothesised that territorial behaviour stabilizes population density around a level set during years of low food. Red squirrels are highly territorial (C. Smith 1968), maintain individual, non-overlapping territories (Gurnell 1984), and they are active year-round (Humphries et *al.* 2005). Red squirrels require a cache of stored food to survive overwinter; in the boreal forest this is often one or more middens of hoarded conifer cones contained within a territory (M. Smith 1968; Kemp & Keith 1970). Territoriality may limit recruitment of individuals into the population, and therefore overall population density (Rusch & Reeder 1978; Klenner 1991). However, no comparison of the effects of population density and food availability on red squirrel population growth rate has been conducted. The ability to quantify annual fluctuations in natural food availability and to accurately census populations creates the unique opportunity to assess the relative support for separate and combined models of food availability and conspecific density on population growth rates.

My objectives were to test the hypotheses that the population growth rate of a territorial species living in a temporally variable food environment will be influenced most strongly by i) population density, ii) food availability or iii) a combination of these. I fit models that used food and density to predict population growth rates. I used life-table response experiments (LTRE; Caswell 1989) to investigate the response of the population growth rate to temporal variation in fertility and survival of female squirrels in four age-classes (yearlings, 2 year-olds, prime-age (3-4 year olds), and older (5+) individuals). LTRE links changes in life-history traits, specifically reproductive success and survival of different age-classed individuals, to the observed population growth rate (Caswell 1989; Brault & Caswell 1993; Cooch et *al.* 2001). While prospective analysis (e.g., sensitivity) show the potential influence of change in vital rates on population growth, retrospective analyses, such as LTRE, use information on changes in the vital rates in response to environmental variability that cause fluctuations in the population growth rate (Caswell 1989). This technique could help link the vital rate component(s) responding to density or food to the observed population dynamics. I also tested if the vital rates showing the highest sensitivity actually make the largest contributions to observed changes in population growth.

My working hypothesis was that red squirrel population growth rates were a function of both food availability as well as conspecific density. Food availability is known to affect individual performance (Boutin 1990; Adams 2001; Ferrer & Bisson 2003) and could directly affect population growth. If red squirrel population growth rates vary with food, I expected territory size to be plastic and inversely related to food availability. Population density could also be an important contributor to population

dynamics, as red squirrel territoriality may impose a bound on population size (Rusch & Reeder 1978; Adams 2001); and may lead to the relatively constant population sizes observed by Rusch & Reeder (1978).

METHODS

STUDY AREA

Two red squirrel populations were studied near Kluane Lake, Yukon, Canada (61°N, 138°W; elevation range: 900 – 950m above sea level) in 18.5ha (plot A) and 36ha (plot B) study sites from 1990 - 2004. The dominant vegetation was mature white spruce (*Picea glauca*), the only conifer in the area (Dale et *al.* 2001). Plot A had lower mature white spruce (i.e., of cone producing size, >5cm diameter at breast height) density ($881 \cdot ha^{-1}$) compared to plot B ($1185 \cdot ha^{-1}$). Along the outside boundary of each study area, either a buffer area of suitable habitat or a sharp transition into unusable habitat (e.g., marsh) was present. Red squirrel movement between the plots was extremely rare (Boutin, unpublished data); therefore, they were considered separate populations.

POPULATION MONITORING

Each May, both populations were censused by capturing all red squirrels using Tomahawk live traps baited with peanut butter and set on squirrel middens (Price et *al.* 1986; Humphries & Boutin 2000). All squirrels were permanently tagged with metal ear tags, and a unique colour combination of electrical wire was threaded through the tags each spring in order to visually identify individuals at a distance. Repeated live trapping and records of territorial calls were used to determine the ownership of all middens. I

quantified the annual spring population density based on the total number of individuals within a standard area of each plot starting in spring 1990. I used this delineation of population density because new middens were occasionally found in marginal habitat and the plots expanded slightly over time. The annual spring census included yearling individuals and older, and is a pre-breeding census since most juveniles of the year had not yet emerged from the nest. Furthermore, those that had emerged were not territory holders when the census was conducted (Boutin, unpublished data). All females were monitored for their reproductive condition (breeder / nonbreeder) based on trapping and palpation for pregnancy status. For breeders, litter sizes and offspring sex was recorded during a nest entry shortly after parturition; therefore all offspring were confidently assigned to a known breeding female. Offspring were uniquely ear-tagged while in the nest and their fates followed (see Humphries & Boutin (2000) for more information on trapping).

FOOD AVAILABILITY

Temporal variation in food availability was based on annual counts of white spruce cones. I assumed cones were a reasonable proxy for the availability of white spruce seed over time. Cone counts were conducted each year on the trees located closest to each of 84 regularly spaced grid stakes located throughout each plot. Counts were done during the last week of July to ensure they were conducted prior to cone harvesting by red squirrels (Peters et *al.* 2003). Cones on the top 3m of each tree seen from one side were counted as a cone index. If there was >100 cones, a photo was taken and cones were counted on the photograph. I converted the cone index to the actual total numbers of

cones present on the sample trees based on the conversion of log(total cones) = 0.073 + 1.189 • log(cone index) (LaMontagne et *al.* 2005; Chapter 2). I calculated cones • ha^{-1} for each year (1989 - 2003) by multiplying the density of live mature white spruce trees in each plot by the mean number of cones per tree in each site. The density and health of trees were based on quadrats sampled throughout the plots in 1996, 2002, and 2004 (LaMontagne & Boutin, unpublished data; also see Chapter 6) to account for variation in total cone production from trees lost to a spruce bark beetle (*Dendroctonus rufipennis*) infestation in the area first detected in 1994 (Garbutt 2002). Values for intervening years were estimated assuming a constant mortality rate between years of quadrat sampling.

MODELS

I assessed the effect of food abundance and population density on red squirrel population dynamics by fitting a series of models to the population growth rate ($r = \ln(N_{t+1}/N_t)$) for each population (Table 4-1). I fit all models using maximum-likelihood estimation. Analyses were based on the female-only fraction of the population. Potential variables in the models included food availability in the fall prior to the spring census (F_{t-1}) as a measure of the resources available to produce and rear offspring in year 't', spring population density as the density dependent factor (N_t), and food availability in the fall of the census year (F_t) that would likely influence survivorship to the following spring (to '*t* + 1'; Figure 4-1). I did not include further cone lags because although red squirrels store cones, over time seeds become less viable for eating (Hurly et *al.* 1987). Autocorrelation functions on population density (Turchin & Taylor 1992) indicated no lags in density were significant and therefore none were included in model fitting. I entered food in the

model as a linear term. I examined the potential for a nonlinear red squirrel numerical response with food using a Michaelis-Menton numerical response term ($\ln(N_{t+1}/N_t) = a + [(e \cdot F_t)/(f + F_t)]$, where 'e' is the maximum population growth rate and 'f' is the half-saturation constant; Fryxell et *al.* 1999). Fit of the Michealis-Menton function suggested that the relationship between the population growth rate and food availability was adequately described by a linear relationship within the range of food densities observed during the study (e.g., Population A: e = 2.08, f ≈1,790,000; χ^2 LRT = 0.420, df = 1, P = 0.518). Therefore, nonlinear responses to food were not presented. Although it may seem intuitive to include a term for per capita food resources, this was not done since the ratio of food to density was driven by food alone. Because of this relationship, it was better to include two variables in the model (e.g., density and food availability) instead of a ratio with them as components (Kronmal 1993).

I estimated the parameters for each model using linear regression analysis in STATA 9.0 (StataCorp 2005). I included variables for population density and food availability both separately and together in models, and used Akaike's Information Criterion with small sample size adjustment (AIC_c; Hurvich & Tsai 1989) to compare model fits to the data (Burnham & Anderson 1998). AIC_c ranks the ability of a suite of models to fit a common set of data and selects for parsimony by penalizing models for each additional parameter included. The model with the lowest AIC_c value is the most plausible model for the data (Burnham & Anderson 1998). As a rule of thumb, models with an AIC_c difference (for model 'i': $\Delta AIC_{ci} = AIC_{ci} - AIC_{cmin}$; where 'min' is the minimum AIC_c value) of ≤2 do not allow the selection of one model over another. Models with ΔAIC_c values of 4 to 7 have less support, and models with ΔAIC_c >10

explain very little of the variation in the data compared to the other models and essentially have no support (Burnham & Anderson 1998). I calculated Akaike weights and used them to determine the best model; they range between 0 and 1 and represent the weight of evidence for each model as compared to the suite of models tested (Burnham & Anderson 1998). AIC_c provides relative model comparisons, but does not provide information on the absolute fit of a model to the observed data (Morris et *al.* 1995, Burnham & Anderson 1998). Fit of the model predictions to the observed population growth rates were based on R^2 from linear regression analyses.

Life-Table Response Experiments

I conducted life-table response experiments (LTRE) with years as random effects to determine the vital rate (fertility, survival) that contributed the most to the population growth rate (Caswell 1989; Caswell 2001). LTRE is a retrospective analysis that uses information on changes in observed vital rates that cause fluctuations in the population growth rate (Caswell 1989). I separated the female portion of the population into four age-classes: (1) yearlings, (2) two-year olds, (3) prime-age individuals (3-4 year olds), and (4) older females (5+ years old), based on survivorship curves and breeding probabilities. Female red squirrels do not consistently breed at one-year of age (Rusch & Reeder 1978); they are typically two-years old at first breeding (Becker 1993). Being a first-time breeder may affect their ability to successfully rear offspring. Most squirrels do not survive to five years old, and the few individuals that do may contribute little to population growth (unpublished data). Lambda ($\lambda = N_{t+1}/N_t$) is the growth rate typically used for LTRE (Caswell 1989; Brault & Caswell 1993; Caswell 2001; Cooch et *al.* 2001;

Oli et *al.* 2001; Oli & Armitage 2004), and is also used here. Because the population data were collected as a pre-breeding census, following Caswell (2001), fertility for each stage class 'i', F_i, was the number of female offspring at '$t + 1$' per female at time t. Fertility therefore represented the proportion of females breeding • mean female-offspring litter size of breeders • proportion of offspring surviving to '$t + 1$'. P_i was the proportion of females surviving and remaining in the same stage, and G_i is the proportion of females surviving and moving into the next stage (Caswell 2001).

The age-class population projection matrix for red squirrels was expressed as:

$$\begin{pmatrix} F_1 & F_2 & F_3 & F_4 \\ G_1 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{pmatrix}$$

Contributions of vital rates to population growth determined by LTRE were comprised of two parts, sensitivity of lambda to the vital rates, and vital rate covariance (Caswell 1989). First, I determined the sensitivity of lambda to each of the mean vital rates (over all years), then I combined the calculated sensitivities with the observed variance - covariance of the vital rates over all years to calculate the contributions of each vital rate to projected lambda. Only individuals present on the study sites in 1990 or born on the sites later were used in LTRE analyses.

RESULTS

POPULATION TRENDS

Over the 15-year study period red squirrel density fluctuated by almost a factor of five (0.82 to 3.98 females·ha^{-1}) in plot A and by a factor of four (0.62 to 2.48 females·ha^{-1}) in

plot B (Figure 4-2). Population A tended to have consistently higher spring densities, with a long-term mean of 1.65 ± 0.22 females·ha^{-1} (mean ± standard error), compared to population B (1.15 ± 0.12 squirrels·ha^{-1}). Both populations had the highest growth rate over a mast year, and their peak densities occurred in the spring following the 1998 cone crop (Figure 4-2).

FOOD AVAILABILITY

White spruce cone abundance varied annually by orders of magnitude during the study, with cone density ranging from a few hundred cones per hectare up to over one million cones per hectare (Figure 4-3). The coefficient of variation for cone production on plot A was 1.37, and plot B was 1.48. White spruce cones were most abundant in the summers of 1993 and 1998 and have been identified as mast years (method from Chapter 3). Plot A consistently had more cones than plot B, similar to the trend in population density. Plot B produced on average 63% of the cones of plot A over the 15 years of the study despite plot A having a lower density of white spruce.

MODEL FITS

Food availability in the current year (F_t) tended to have a larger effect on red squirrel population dynamics than red squirrel density (N_t) or cone density in the previous year (F_{t-1}). Of the eight models, the model with the most support was the same for both populations and included variables for both red squirrel density and food (DD+F) in characterizing red squirrel population dynamics (Table 4-2). This model had the highest Akaike weight (w_i) of 0.669 for population A and 0.653 for population B; with w_i's about

3.7 and 4.7 times greater than the next closest model for both populations, the food only (F) model. Predictions from the density and food (DD+F) model explained 70% of the variation in the observed population A growth rate, and 65% for B. The food only (F) model, represented white spruce cone availability in fall of the census year 't' and positively influenced population growth (Table 4-3), explaining 51% of the variation in observed growth rate for population A and 43% for B. This model had a ΔAIC_c of 2.64 and a w_i of 0.179 and a ΔAIC_c of 3.08 and a w_i of 0.142 for populations A and B, respectively. The top four models based on AIC_c all included food in year '*t*' in the model (Table 4-2).

Red squirrel spring population density had a negative effect on population growth (Table 4-3). The density only (DD) model explained 14% of the variation in population growth rates for red squirrel population A, had a ΔAIC_c of 17.04, a very small w_i (0.003), and was ranked seventh of the eight models compared. This model was the fifth best of the eight models compared for population B, with a ΔAIC_c of 5.69, and was not highly weighted ($w_i = 0.039$). The density of female squirrels in year '*t*' explained 30% of the variation in the population growth rate.

To put these model fits in perspective, the best model for population A included both conspecific density and food availability in year '*t*' (DD+F), and based on Akaike weights it was over 200 times more likely than the red squirrel density only model (DD) in explaining the observed variation in red squirrel population growth rates. Furthermore, the food alone (F) model was favoured 60 times more than the model with red squirrel density alone (DD). The best model for population B (DD+F) was favoured 17 times more than the density only (DD) model, and the food only (F) model was

favoured about 3.5 times more than density alone. Although the populations had the same top two models, density alone (DD) explained twice as much of the variation in the observed population growth rate for squirrel population B compared to A. Partial R^2 of the best model (DD+F) showed that 65% of the variation in population growth was explained by food in 't' after accounting for density in population A, while 27% of the variation was explained by density after accounting for food. This was 50% for food and 40% for density for population B growth rate while controlling the other factor.

The model for lagged food (LF; resources available in 't - 1') was ranked sixth and seventh for populations A and B, respectively, with w_i's of 0.004 and 0.011 and explained 15% and 17% of the variation in the observed growth rates for (Table 4-2a). The lag in food availability term (F_{t-1}) was correlated with population density in year 't' (Spearman correlations; population A = 0.724; B = 0.747), and therefore the DD and LF models explained about the same amount of variation in the population growth rate for population A. DD explained twice the variation that the LF model did for population B. Partial R^2 for models including conspecific density and lagged food (DD+LF) showed that each of these terms only explain 2% of the variation after controlling for the other for population A, while for population B, after controlling for cones, red squirrel density explained 16% of the variation in the growth rate, and after controlling for density, lagged cones explain no further variation. For both populations, the model including both red squirrel density and lagged cone availability terms (DD+LF) was ranked last of the models tested. The sum of the Akaike weights for all models with food (F_t), or density (N_t), or lagged food (F_{t-1}) were equal to 0.99, 0.73, and 0.14, respectively for population A, and 0.93, 0.77, and 0.14 for population B. This suggests again that the best

model of those considered contained food in year '*t*', and that there was a low probability of the best model including lagged food.

LIFE-TABLE RESPONSE EXPERIMENTS

For each population, the sensitivity of the population growth rate (lambda) to female red squirrel vital rates based on the mean matrix for the four age-classes over all years (with only sensitivities for the non-zero transitions shown; populations are subscripted, see Appendix 1 for the mean matrices) was:

$$S_A = \begin{pmatrix} 0.364 & 0.245 & 0.265 & 0.134 \\ 0.456 & \cdots & \cdots & \cdots \\ \cdots & 0.212 & 0.229 & \cdots \\ \cdots & \cdots & 0.198 & 0.100 \end{pmatrix}$$

$$S_B = \begin{pmatrix} 0.345 & 0.266 & 0.323 & 0.136 \\ 0.361 & \cdots & \cdots & \cdots \\ \cdots & 0.266 & 0.323 & \cdots \\ \cdots & \cdots & 0.128 & 0.054 \end{pmatrix}$$

The population growth rate (lambda) for both populations was most sensitive to the survival (G_1) and fertility (F_1) of yearlings. Lambda for population B had similar sensitivities to these terms plus fertility and within-age-class survival for prime-age (3-4 year old) individuals (F_3 and P_3). The lowest sensitivity for both populations was to survival of females in the oldest age-class (P_3). Based on the vital rate sensitivities and the observed fluctuations in the vital rates, the LTRE contributions to lambda (see 'C' matrices below) showed that fertility of two-year old females (F_2) had the largest contribution to the variation in the projected lambda of 39% and 35% for populations A

and B, respectively. This vital rate was not among those that showed the highest sensitivity. Fertility of yearlings (F_1) and prime-age females (F_3) also contributed much more than the other vital rates. Together these three fertility terms explained 73% and 70% of the variation in the projected growth rates for populations A and B, respectively. Including fertility of the oldest females further increased this to 81% and 78%. The transition to the oldest age-class and survival of these females had the smallest contributions to population growth. The transition to the oldest age class (G_3) had negative contributions to lambda, due to negative covariance with many of the other vital rates. The matrix of all vital rate contributions for each plot, scaled to sum to 1 was:

$$C_A = \begin{pmatrix} 0.161 & 0.392 & 0.175 & 0.086 \\ 0.048 & 0 & 0 & 0 \\ 0 & 0.077 & 0.058 & 0 \\ 0 & 0 & -0.017 & 0.021 \end{pmatrix}.$$

$$C_B = \begin{pmatrix} 0.207 & 0.348 & 0.149 & 0.073 \\ 0.049 & 0 & 0 & 0 \\ 0 & 0.080 & 0.083 & 0 \\ 0 & 0 & -0.005 & 0.017 \end{pmatrix}$$

Fertility vital rates included the lower-level vital rates of the proportion of females within the age-class that bred, the litter size of breeding females, and survival of juveniles until the census the following spring (Appendix 2). Of these, food availability in the fall of '*t*' would affect only juvenile survival to the next census; suggesting this component of fertility had the most affect on population growth. Of the three lower-level vital rates, the proportion of females breeding within an age-class had the lowest variability (with

the exception of yearling female breeders), followed by litter size. Juvenile survival was the most variable lower-level fertility vital rate.

DISCUSSION

EFFECTS OF FOOD & DENSITY ON POPULATION GROWTH

The results here show that red squirrel population growth rates were affected by both food availability in fall of the current (not previous) year and conspecific density. Together, upwards of 70% of the variation in population growth rates was explained by a model including both terms. In this model food availability in year 't' was the dominant factor and explained up to 65% of the variation in the population growth rate after controlling for red squirrel density; red squirrel density explained up to 40% of the variation, after variation in food availability was controlled for. This differed for each population. I predicted that density could have a strong effect on population dynamics, based on previous studies (Rusch & Reeder 1978; Fryxell et *al.* 1998) and the highly territorial nature of red squirrels (C. Smith 1968; Rusch & Reeder 1978). However, the results suggest that it was unlikely that density alone was sufficient to explain growth of the red squirrel populations studied here. Fryxell et *al.* (1999) and Choquenot & Ruscoe (2000) similarly found that population density and food availability both contributed to affect population growth rates of marten (*Martes americana*) and the wild house mouse (*Musmusculus* L.), respectively.

Including conspecific density in the model tended to enhance the depression of the population growth rate more than low food alone (Appendix 3), especially the year following the cone mast when cone production was low and spring population density

was high. Population density also played a role in the growth rate of mouse populations potentially through intraspecific competition for food, or effects of predators, parasites, or disease (Choquenot & Ruscoe 2000). The spring following a mast year had increased population densities, but the next year they were at similar levels as prior to the mast. This pattern could be due to the effect of population density, but it is also the case that mast years are most often followed by a low seed production year (Greene & Johnson 2004). I discuss this further in the 'Territoriality & Population Dynamics' section below.

In the 15 years of census data analysed, red squirrel population density varied by up to a factor of five, with the highest population growth rate and density typically coinciding with spruce cone masts. Other species have also been known to peak in density following a resource pulse (Wolff 1996; Ostfeld & Keesing 2000; Wauters et *al.* 2001). Red squirrel density has also been shown to respond positively to food supplementation (Sullivan & Sullivan 1982, Sullivan 1990, Klenner & Krebs 1991). A positive association of population growth rates and food levels contradict the conclusion of Rusch & Reeder (1978) that red squirrel population density should be maintained around a density set during years of scarce food. Rusch & Reeder (1978) reported temporal variation in cones over their four-year study, however their study area was comprised of mixed spruce and jack pine (*Pinus banksiana*) stands. Jack pine has relatively small annual fluctuations in cone production, and serontinous cones that remain on trees for multiple years (Rudolph & Laidly 1990). Mixed stands may have lower variability in annual seed production due to species differences in reproductive patterns compared to this study where white spruce was the only conifer species. The discrepancy in the population patterns observed could be due to habitat differences, differences in the

magnitude of cone production observed in the studies, or study duration. Rusch & Reeder's (1978) study spanned four years; if the study here was conducted over a similarly short amount of time the mast seeding years could have been missed.

It was unexpected that cones in year '*t* - 1' explained so little of the variation in red squirrel population growth from year '*t*' to '*t* + 1'. Lagged cones were included to represent the food resources that would be available to females for reproduction in spring of year '*t*'. Food availability has been shown to influence an individual's body condition, breeding success, and survival (Rognmo et *al.* 1983: Dobson & Kjelgaard 1985; Boutin 1990; Chapter 6). Fertility contributed most to the projected growth rate, but the components of fertility, particularly the proportion of females breeding and annual mean litter size varied relatively little. Red squirrels in this study may use a strategy of consistently producing a litter each spring, because they live in a variable food environment (Orzacki & Tuljapurkar 2001). During a series of relatively low-cone years (2002-2004), an individual's territory size and the number of cones in the territory had little effect on whether or not a female red squirrel produced a litter (Chapter 6). An individual's fitness would be increased if a cone mast occurred, accompanied by high juvenile recruitment into the population. Cones in year '*t*' were the only factor I considered that would influence the juvenile overwinter survival component of female fertility.

I considered fluctuations in the red squirrel population growth rate to be the result of births and deaths of individuals, as opposed to immigration and emigration. This was because buffers of suitable habitat or sharp habitat transitions comprised study site boundaries. The specific effects of predation, disease and parasites, and weather

conditions were not considered here. The main red squirrel predators in the area are goshawks (*Accipiter gentilis*) and lynx (*Lynx canadensis*; Boonstra et *al.* 2001). Predator-removal experiments suggest red squirrel populations maintain relatively constant densities through compensation for lost individuals (Stuart-Smith & Boutin 1995). The effect of disease and parasites on red squirrels is unknown. Red squirrels are active year-round, even in extremely low temperatures (Humphries et *al.* 2005); therefore weather, and specifically winter weather, may have only a small effect on population dynamics, but this has not been tested.

VITAL RATE SENSITIVITIES & CONTRIBUTIONS TO POPULATION GROWTH

Although fertility contributed the most to the projected population growth (up to 80% if females of all ages were considered) the sensitivity of population growth rate to survival of yearling to two-years of age was the greatest. However, because yearling survival did not vary greatly during the study, it contributed little to the projected population growth. It is not uncommon for vital rate components with the greatest potential impact on the population growth rate to have lower temporal variability than vital rates with low sensitivity (Gaillard et *al.* 2000). For many ungulate species, the population growth rate is most elastic to adult survival; but this vital rate often has low temporal variability (Gaillard et *al.* 1998; Gaillard et *al.* 2000; Coulson et *al.* 2005). It has been suggested that juvenile survival contributes much more to population growth rates than adult survival (Gaillard et *al.* 1998). After discontinuing a food addition experiment, Klenner & Krebs (1991) saw drastic red squirrel population declines. Since their adults maintained high survivorship rates (range: 86-95%) they concluded the population

declines were due to loss of juveniles through mortality or emigration. This is similar to the results here; fertility (most likely the component of juvenile survival to spring of 't + 1') contributed most to population growth. Interestingly, it was recruitment of juveniles into the population (or mortality of nonterritorial squirrels) that was similarly suggested by Rusch & Reeder (1978) as the factor that led to spring-to-spring stability in population density.

For the two red squirrel populations studied here there was little variation in the contribution of vital rates to population growth. This was expected, as these populations experienced similar patterns of variation in their primary resource. However, populations of the same species subjected to different environmental conditions may have different vital rates with different contributions to the population growth rate (Coulson et *al.* 2005). For example, in one bighorn sheep (*Ovis canadensis*) population, adult survival was high and variable due to the effect of disease, and this vital rate contributed three times as much to the variation in population growth compared to another population where adult survival was high and constant. In another population, lamb overwinter survival was variable and affected by population density (Coulson et *al.* 2005). Environmentally related differences in vital rate contributions to population growth rates were also detected in populations of Columbian ground squirrels (Sp*ermophilus columbianus*) at different elevations (Dobson & Oli 2001). Both Coulson et *al.* (2005) and Dobson & Oli (2001) suggest that understanding the source of environmental variation affecting vital rates and in turn affect population growth rates is key, and should be the focus of future research. Red squirrel populations experiencing different patterns of resource variability, like the bighorn sheep and Columbian ground squirrels above,

may show different vital rate contributions to population growth. For red squirrels this could include a population with more constant temporal food availability compared to a population exposed to mast seed resource pulses. Environmental variability could also include climatic variation that affects vital rates directly, or indirectly through resource availability (e.g., rainfall and pasture growth; Davis et *al.* 2002).

TERRITORIALITY & POPULATION DYNAMICS

Populations of some territorial species are relatively constant in abundance over time, while others fluctuate depending on the magnitude of other ecological effects (Fryxell et *al.* 1999). Territoriality may limit recruitment of individuals into the population, and therefore overall population density (Rusch & Reeder 1978; Patterson 1980; Klenner 1991). Klenner (1991) found that red squirrels did not reduce their territory size in food-supplemented populations, while Saitoh (1991) found territory size decreased in grey red-backed voles with higher food conditions. Rusch & Reeder (1978) suggested that red squirrel territory size was constant over space and time, being set by food supply in low seed production years. Stable population sizes may also occur if territories are based on breeding sites and are not food-based territories (Morse 1980). However, if territory size fluctuated with food, increased food may reduce territory size, followed by subsequent population increases (Hixon et *al.* 1983). Plasticity in territory size could lead to the smaller effect of density as compared to food on red squirrel population growth rate. In population B, mean female spring territory sizes varied from < 0.1ha to >0.5ha from 1990 to 2004 (Figure 4-4; Boutin, unpublished data), inversely with population density. This variation in red squirrel territory size over time contradicts other studies of red squirrel

territory size (Rusch & Reeder 1978, Klenner 1991). Because spring population density was correlated with food availability in the previous fall, then food is also correlated to spring territory size.

The influence of food and conspecific density on population growth may arise from the behaviour of female red squirrels to sometimes give part or all of their territory to one or more offspring (Berteaux & Boutin 2000). If, when cones are very abundant, like during a mast year, females give more of their territory to offspring, this could result in smaller territory sizes, higher juvenile survival (Berteaux & Boutin 2000), and a subsequent increase in the population growth rate. Or, increased intruder pressure through the presence of many juveniles and increased population density during mast years should create conditions whereby the population growth rate could also be influenced by both food and density. High overwinter survival following a cone mast would maintain small territories. As mentioned, mast years are typically followed by low seed years (Greene & Johnson 2004), and at this point territories may be too small to provide adequate resources in the post-mast year, and the population growth rate declines more than it would based on food resources alone (Appendix 3).

Plasticity in territory size may diminish the effect of density until the minimum territory size is reached. Given that territory size seemed to be plastic and responded to food availability, population increases may be observed when food availability was high; the environment could support more individuals, if only for a short time. At this point, space would become the factor in least supply, and the population would not increase further. On the other hand, with a fixed territory size, population density should remain fairly constant. The mechanism for constant population size would be the exclusion of

excess individuals; when there is no more room for additional territories within the population, non-territory holders either die or emigrate from the population (Rusch & Reeder 1978). Wauters & Lens (1995) showed that the per-capita reproductive rate of Eurasian red squirrels (*Sciurus vulgaris*) in conifer forest was affected by female density. At high population densities female Eurasian red squirrels not occupying territories become "floaters"; few floater females breed, reducing the overall per capita reproductive rate. Eurasian red squirrels have a different pattern of space use than North American red squirrels, with females of the former having some home range overlap with other individuals of the same sex, and exclusive core areas (Lurz et *al.* 2000). In lower quality deciduous habitat, Wauters & Lens (1995) found that food had a stronger effect than density on the ability of juveniles to survive until weaning. The presence of floaters may explain why population density may have a stronger effect than food availability on reproduction in the Eurasian red squirrel than detected here with North American red squirrels where there were no floaters in the population.

FOOD LIMITATION IN RED SQUIRRELS

To put this study in the context of population regulation and factors preventing continuous population growth (Krebs 2002), the results of this study on red squirrels point more towards food availability than population density. Model inspection showed that with constant food availability, the squirrel population increased (or decreased) exponentially. For example, maintaining a population at mast seed levels (e.g., based on plot A) and starting with 1 squirrel per ha predicted 14000 squirrels per ha in 20 years. Including variability in food greatly slowed the trajectory of population increase, with

some periods of population decline with low food; the precise trajectory depended on the food levels and the pattern of variability. This pattern is likely to occur among species that rely primarily on a highly variable, or pulsed, food source, with high potential population growth rates with only a minor influence of population density. For example, mast seeding leads to marked increases in populations of wild boar (*Sus scrofa*; Bieber & Ruf 2005), white-footed mouse (*Peromyscus leucopus*) and eastern chipmunks (*Tamias striatus*; Wolff 1996), and red kangaroo (*Macropus rufus*) population growth is strongly influenced by vegetation dynamics due to variable rainfall (Caughley & Gunn 1993). Density models assuming a constant environment show logistic growth to a carrying capacity, returning to this density following population perturbations.

A long-term food addition experiment would be useful to look at the effects of food and population density on the red squirrel population growth rate when food is superabundant for not only one-year, like a cone mast, but for multiple years. I predict that population size would increase, with a corresponding decrease in territory size, until the minimum territory size was reached. If the food-addition persisted long enough the territorial social structure could eventually breakdown if red squirrels viewed their environment as temporally homogeneous, since spatial and temporal variability in food is thought to be the ultimate cause for territoriality in red squirrels (Rusch & Reeder 1978).

Long-term data on population density may not be enough to investigate the role of density on population growth, as populations that show a limited range in densities will provide little insight (Krebs 2002). Although the data here spanned 15 years, the relative rarity of mast years generated few peak red squirrel population densities. Longer-term studies including more mast years, and studies focusing on the determinants of territory

size in red squirrels, especially spanning seed masts would be useful to understand the potential role of territory size plasticity in response to food as a contributing factor behind population fluctuations. Red squirrels occupy a variety of forest types, including mast-seeding conifers such as white spruce, to multiple species combining for smaller fluctuations, or single species with more consistent seed availability such as jack pine. In areas with more consistent food availability, population density, territory size, and fluctuations in fertility would be expected to be lower than when red squirrels occur in more variable environments. The contributions of different vital rates to population growth may vary in these habitats, because of the differences in environmental variability (Coulson et *al.* 2005).

Natural populations do not exist in a constant, static environment, so it is unlikely that density or food would act in isolation to drive population dynamics. If the environment fluctuates continuously, population density in the area would be expected to fluctuate in response to the changes in the capacity of the habitat to support individuals (White 2001). Here, I showed that population growth rates were best described when both food and density were included. Few other studies have assessed the relative influence of population density and food availability on population growth rates (but see Choquenot 1998; Fryxell et *al.* 1999; Choquenot & Ruscoe 2000). Although many studies have been conducted to look for population density feedback (e.g. Brook & Bradshaw 2006), multiple hypotheses for population dynamics are rarely tested simultaneously (Choquenot 1998; Newton 1998; Krebs 2003). More research focusing on both observational studies with good resource and population density estimates, and experimental studies may provide further insight into how food availability and

population density separately and together contribute to the range of dynamics seen in nature.

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Table 4-1: Population models fit to data. 'N' is the spring female red squirrel population density (per ha^{-1}), and 'F' is white spruce cone crop density recorded in July (per ha^{-1}) of years '$t-1$' and 't'.

Model	Equation
Density & Food independent (DFI)	$\ln (N_{t+1}/N_t) = a + \varepsilon_t$
Density dependent (DD)	$\ln (N_{t+1}/N_t) = a + b \cdot N_t + \varepsilon_t$
Lagged food only (LF)	$\ln (N_{t+1}/N_t) = a + c \cdot F_{t-1} + \varepsilon_t$
Food only (F)	$\ln (N_{t+1}/N_t) = a + d \cdot F_t + \varepsilon_t$
Density dependent + Lagged food (DD+LF)	$\ln (N_{t+1}/N_t) = a + b \cdot N_t + c \cdot F_{t-1} + \varepsilon_t$
Density dependent + Food (DD+F)	$\ln (N_{t+1}/N_t) = a + b \cdot N_t + d \cdot F_t + \varepsilon_t$
Food with time lag (LF+F)	$\ln (N_{t+1}/N_t) = a + c \cdot F_{t-1} + d \cdot F_t + \varepsilon_t$
Density dependent + Lagged food + Food (DD+LF+F)	$\ln (N_{t+1}/N_t) = a + b \cdot N_t + c \cdot F_{t-1} + d \cdot F_t + \varepsilon_t$

Table 4-2: AIC_c results and Akaike weights (w_i) for population dynamics models based on female-only red squirrel population growth for a) population A and b) population B. See table 4-1 for the explanation of the models. The "Rank" score is based on w_i . 'n' is the number of parameters in each model, and R^2 is the fit of the predicted and observed population growth rates.

Rank	Model	n	AICc	ΔAICc	w_i	R^2
a) Population A						
1	DD+F	4	6.54	0.00	0.669	0.70
2	F	3	9.17	2.64	0.179	0.51
3	LF+F	4	10.77	4.23	0.081	0.59
4	DD+LF+F	5	11.42	4.89	0.058	0.70
5	DFI	2	15.90	9.37	0.006	0.00
6	LF	3	17.01	10.47	0.004	0.15
7	DD	3	17.04	10.51	0.003	0.14
8	DD+LF	4	20.69	14.15	0.001	0.17
b) Population B						
1	DD+F	4	11.49	0	0.665	0.65
2	F	3	14.58	3.08	0.142	0.42
3	DD+LF+F	5	16.21	4.71	0.063	0.66
4	LF+F	4	16.32	4.83	0.059	0.51
5	DD	3	17.19	5.69	0.039	0.30
6	DFI	2	18.96	7.47	0.016	0.00
7	LF	3	19.70	8.20	0.011	0.17
8	DD+LF	4	21.23	9.74	0.005	0.30

Table 4-3: Parameter estimates of the best-fit model, density and food (DD+F), with the highest AIC_c weights in model fitting, and the density only (DD) and food only (F) models for red squirrel population growth rate. Values in brackets are the 95% confidence interval. See Table 4-1 for the form of the models.

	Parameter estimates			
Model	a	b	d	ε_t
a) Population A				
DD+F	0.0939 (-0.1802, 0.3680)	-0.1849 (-0.3247, -0.0452)	$7.51 \cdot 10^{-7}$ ($4.23 \cdot 10^{-7}$, $1.08 \cdot 10^{-6}$)	0.0383
DD	0.2561 (-0.1701, 0.6822)	-0.1623 (-0.3867, 0.6204)		0.1085
F	-0.2137 (-0.3901, -0.0372)		$7.21 \cdot 10^{-7}$ ($3.22 \cdot 10^{-7}$, $1.12 \cdot 10^{-6}$)	0.0619
b) Population B				
DD+F	0.3321 (-0.0875, 0.7516)	-0.4364 (-0.7529, -0.1199)	$8.43 \cdot 10^{-7}$ ($3.46 \cdot 10^{-7}$, $1.34 \cdot 10^{-6}$)	0.0547
DD	0.5698 (0.0336, 1.1059)	-0.4982 (-0.9244, -0.0720)		0.1097
F	-0.1976 (-0.4058, 0.0106)		$9.22 \cdot 10^{-7}$ ($3.12 \cdot 10^{-7}$, $1.53 \cdot 10^{-6}$)	0.0910

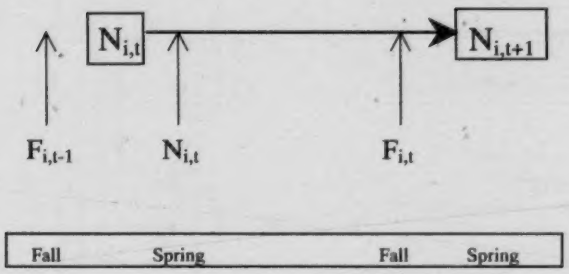

Figure 4-1: Schematic of the relationship of variables input into the population models where $N_{i,t}$ is the spring female red squirrel population density (per ha) of population 'i' in year "t", $N_{i,t+1}$ is the spring population density in year "t+1". $F_{i,t-1}$ is the mean number of cones produced per ha in the summer of year "t-1" within the area occupied by population 'i', and $F_{i,t}$ is the mean number of cones produced per ha in the summer of year "t". The growth rate of population 'i' was calculated as $\ln(N_{i,t+1}/ N_{i,t})$.

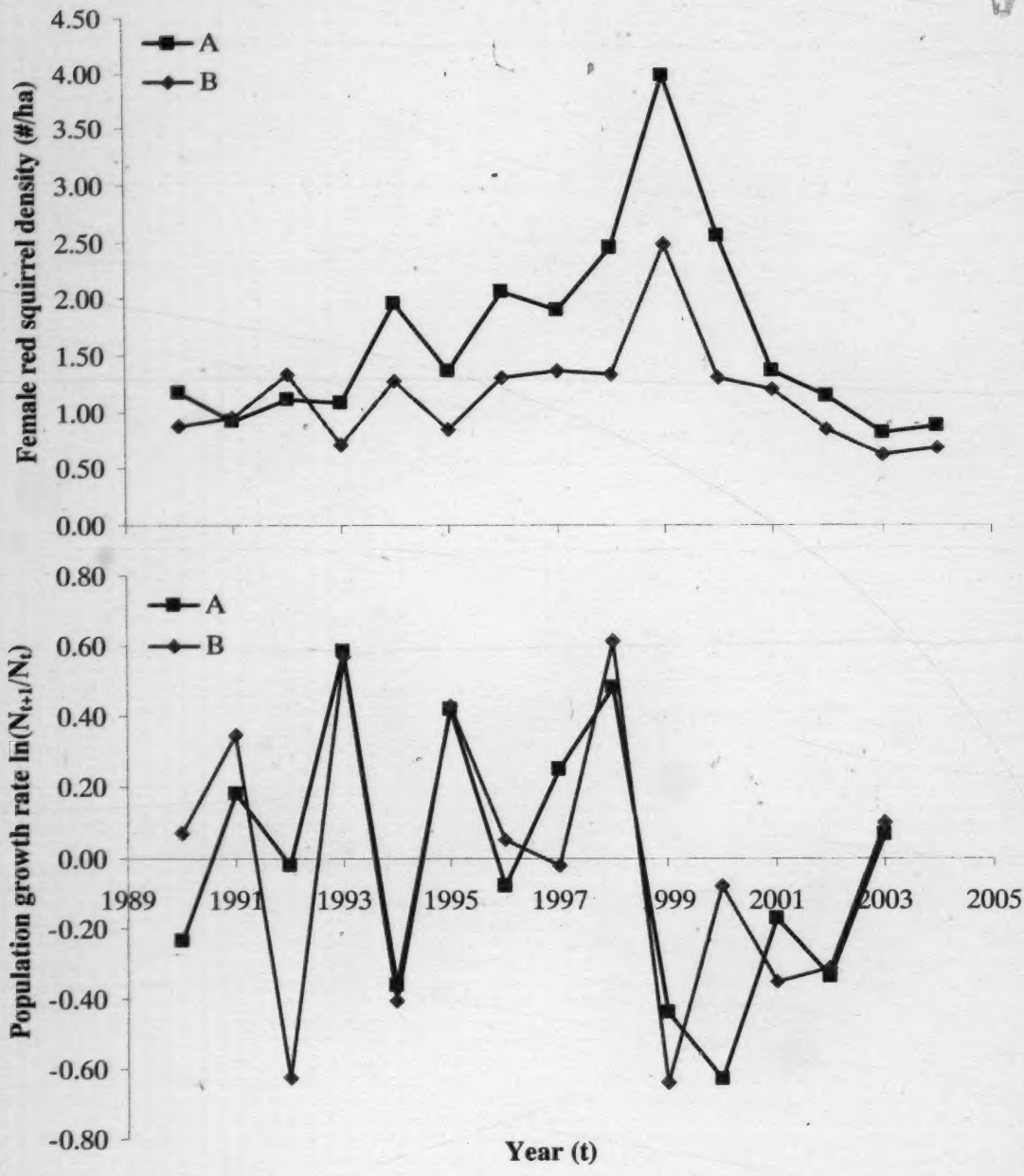

Figure 4-2: Time series (top panel) and population growth rates (lower panel) for two red squirrel populations in the southwest Yukon (1990 - 2004). Data are based on spring (May) censuses of female red squirrels.

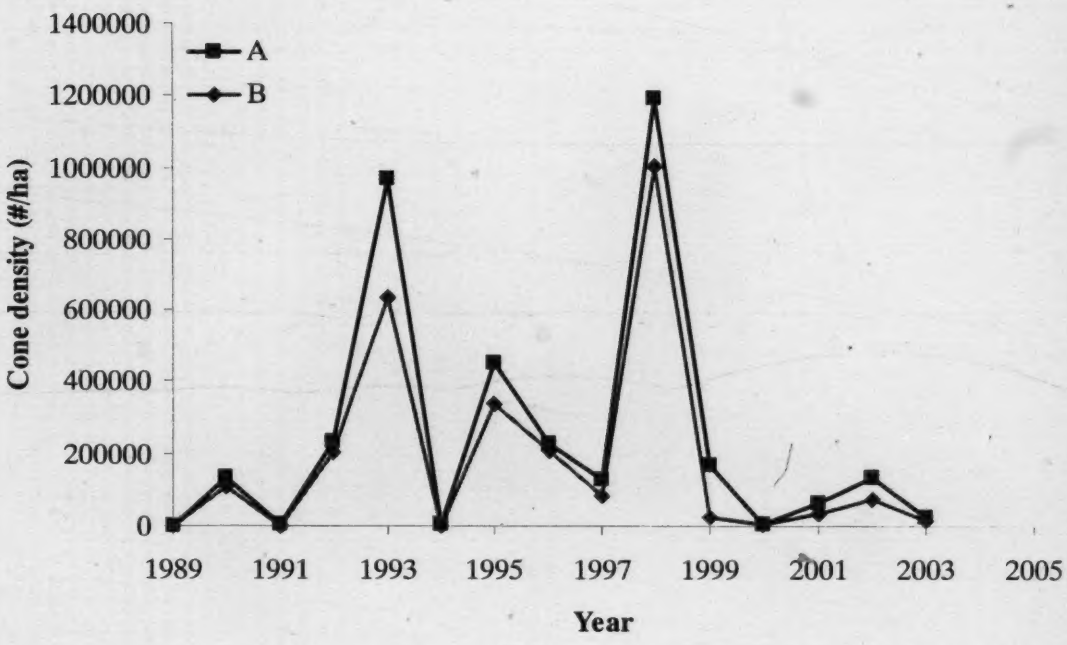

Figure 4-3: Abundance of white spruce cones present on trees (# cones·ha^{-1}) based on visual counts of sample trees and the density of mature white spruce on each study grid from 1989-2003.

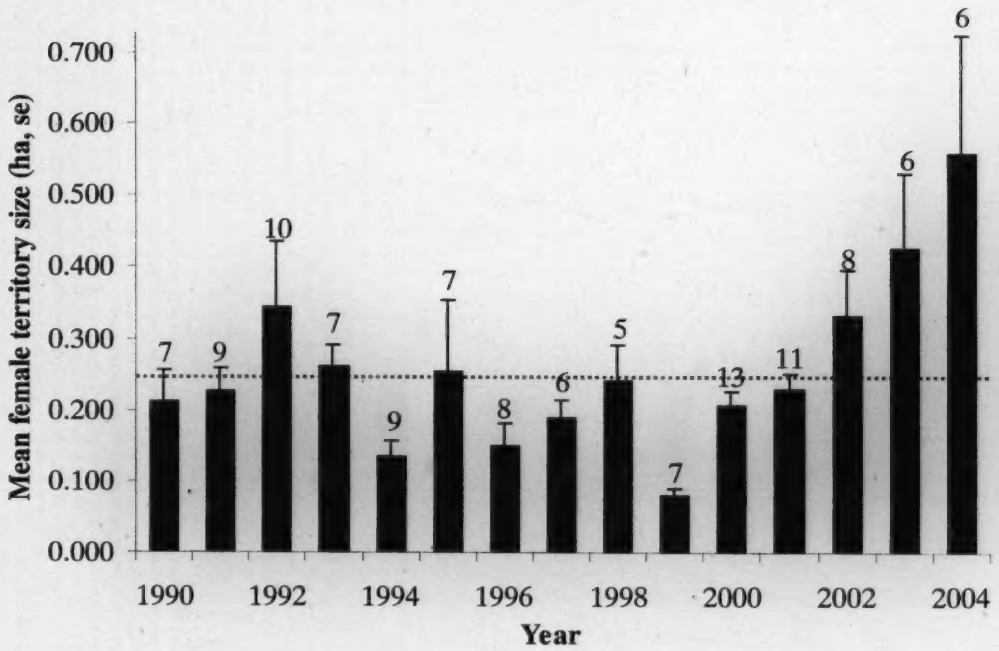

Figure 4-4: Annual mean (± standard error) spring territory sizes of female red squirrels sampled from a 9ha area of plot B from 1990-2004. At least 11 territorial locations were used in generating 100% minimum convex polygon territory sizes. Within each year there was no significant effect of the number of mapping points on territory size. The horizontal line is the long-term mean and number above each bar shows the number of territories mapped (Boutin, unpublished data).

CHAPTER 5

LOCAL-SCALE VARIABILITY AND SYNCHRONY IN MAST SEEDING OF WHITE SPRUCE

INTRODUCTION

Mast seeding is defined as the synchronous and highly variable production of seed crops by a population of plants from year to year (Kelly 1994). The critical components of mast seeding are high variability in seed production and high synchrony. Mast seeding is well documented in a number of plant species, with synchrony detected in seed production between populations over large geographic areas, up to 2500km for *Pinus* spp. (Koenig & Knops 1998). Several hypotheses have been proposed to explain synchronous seeding by individuals within populations; seed predator satiation and increased pollination efficiency having the most support (reviewed in Kelly 1994; Kelly & Sork 2002). Mast seeding may satiate seed predators such that individual plants experience higher reproductive success (Janzen 1971; Silvertown 1980; Kelly 1994), or increased individual pollination success (reviewed in Kelly & Sork 2002). As individuals become synchronized, selection should act against asynchronized individuals thereby enhancing selection for high degrees of synchrony (Janzen 1971).

Individual plants generate the population patterns observed. Individual plants are the unit of selection, and for mast seeding to occur, individuals comprising the population must undergo the same pattern of seed production, increasing and decreasing together. However, most studies have focused on population-level estimates of inter-annual

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variability (Kelly 1994; Herrera 1998). Long-term studies on individual plants, and studying the local-scale extent of mast seeding have been suggested as important directions for research on mast seeding (Kelly 1994; Herrera 1998; Herrera et *al.* 1998; DeSteven & Wright 2002; Kelly & Sork 2002; Buonaccorsi et *al.* 2003; Koenig et *al.* 2003; Liebhold et *al.* 2004). Information on the individual behaviour of plants, their variability and the levels of synchrony, can help in developing mechanistic explanations of mast seeding more than studies at the population level alone (Herrera 1998). Koenig et *al.* (2003) suggested that the levels of individual variability and synchrony may be affected by various selection pressures (e.g. wind vs. animal pollination and dispersal, localized vs. regional seed predators). Variation in seed production patterns among individuals may arise because, in addition to regional weather patterns (Selås et *al.* 2002), seed production is influenced by individual attributes including tree size (Greene & Johnson 1994; Greene et *al.* 2002), local environment (e.g. basal light, Greene et *al.* 2002), and available nutritional reserves (Nienstaedt & Teich 1972).

Temporal and spatial patterns of variability and synchrony are also relevant to ecosystems because of the importance of seed as a food source for wildlife whose population dynamics, and even community-level dynamics may be affected by seed crop availability (Koenig & Knops 2000; Ostfeld & Keesing 2000). Spatial variation in synchrony of seed production by individual trees over relatively small scales (<10km) has been studied in *Quercus* spp. (Koenig et *al.* 1999; Leibold et *al.* 2004). Here, I describe seed production of individual *Picea glauca* (Moench) Voss (white spruce) trees measured over 16 years separated by distances of 30m to 5 km. *Picea glauca* is a wind-pollinated and wind-dispersed mast seeding conifer species; the seeds are a food source for many

small mammals and birds (Dale et *al.* 2001). I address two questions: 1) How does seed production vary between and within years? and 2) How synchronized are patterns of seed production between trees? I focused on levels of synchrony between individuals with increased distance between them and/or whether or not a mast crop was produced.

METHODS

STUDY SPECIES

I studied *P. glauca* in the boreal forest region of the southwestern Yukon Territory, Canada (61°N, 138°W). Here, *P. glauca* has years of complete cone failure, when virtually all trees produce no cones, years of low-intermediate cone production, and mast years (Dale et *al.* 2001). The study area (~5.3km maximum extent) ranges from 850 – 950m elevation and experiences low precipitation (annual mean = 230 mm) falling primarily as rain during summer; mean snowfall is 100cm (Krebs & Boonstra 2001). Vegetation is dominated by *P. glauca*, the only conifer species in the area, with *Populus tremuloides* Michx. (trembling aspen) and a shrub understory dominated by *Salix glauca* L. (grey willow). The dominant *P. glauca* vertebrate seed predator in the area is red squirrel (*Tamiasciurus hudsonicus*), caching thousands of cones annually (Smith 1968). Other vertebrate seed predators are boreal red-backed voles (*Clethrionomys rutilus*), white-winged crossbills (*Loxia leucoptera*), boreal chickadees (*Parus hudsonicus*), and bohemian waxwings (*Bombycilla garrulus*) (Smith & Folkard 2001).

DATA COLLECTION

I measured the annual cone production of *P. glauca* trees at 371 locations from 1990-2005. Tree locations were distributed over 4 study plots; plot A was 17 ha, and plots B, C, and D were each 36 ha (Figure 5-1). Grid patterns (30m) were established over each plot and sampled trees were selected based on the closest tree to a specified grid location. A minimum distance of 30m, and a maximum distance of approximately 5.3 km separated sampled trees. All trees sampled had a diameter at breast height > 5cm, the size at which *P. glauca* may produce cones in this area (LaMontagne & Boutin, unpublished data). Cone production for each tree was estimated by counting the number of cones visible to an observer standing on one side of the tree. This was converted to 'total' cones using Total cones = 10^(0.073 + 1.189 · log(visible cones)) (LaMontagne et *al.* 2005; Chapter 2). Total cone number was used in analyses. I counted cones in late July-early August of each year, prior to cone harvesting by red squirrels (Peters et *al.* 2003). If a marked tree died it was replaced by the next closest live tree. Only one tree per location (the tree measured for the most years; range 5-16 years; mean 11.8 years; median 13 years) was used in my analyses. This avoids pseudoreplication with respect to the correlation and distance classes. No cone data were available for plot D in 1996 and 1997, and some locations in this plot were not sampled after 1995. Fifteen locations (trees) were excluded from analyses having never reproduced (following Koenig et *al.* 2003); the total number of individual trees used in my analyses was 356.

VARIABILITY IN CONE PRODUCTION

For each study plot I calculated the mean annual total cone production plus the standard deviation and the coefficient of variation of the annual means as measured over all years of the study (CV_p = Overall plot SD / Overall plot mean). I also measured individual variability by calculating the average cones produced by an individual across all years plus the standard deviation and the mean coefficient of variation across years for each individual within a plot ($\overline{CV}_i$; Herrera 1998). In addition, for each year, within each plot, the CV of the cone production within a year was calculated as CV_A = Annual plot SD / Annual plot mean. To test the consistency of plot productivity over time I used Kendall's coefficient of concordance, including only those years when all plots had cone counts measured (1991-1995 and 1998-2005). I also calculated the lag autocorrelation function of cone production (ACF_t, where 't' represents the lag) after log transforming and differencing the mean annual total cones per tree within a plot, to fit assumptions of normality and stationarity (Berryman 1999), for each of the plots. Gaps in the data were not interpolated and were not included in ACF analysis. No lags greater than five years were examined due to the length of the data set.

INDIVIDUAL SYNCHRONY IN CONE PRODUCTION

Tests of synchrony in cone production of individual trees over years were conducted based on a modified correlogram (Koenig 1999). First, cone production patterns of all pairs of individual trees over time were correlated to each other using Spearman rank correlations (r_s). Previous studies have used Pearson correlations to test for synchrony (e.g. Schauber et *al.* 2002; Buonaccorsi et *al.* 2003; Koenig et *al.* 2003), but my data were

not bivariate normal distributed (in 332 of 356 cases; Shapiro-Wilk test) and in many cases also violated the linearity assumption of Pearson correlations (Zar 1999). Under these circumstances Spearman correlation is a more robust test (Quinn & Keough 2002). I refer to the Spearman coefficients as levels of synchrony. I examined spatial synchrony of cone production patterns within distance classes between trees (<75m, 76-150m, 151-300m, 301-500m, 501-1000m, 1001-2000m, 2001-3000m, 3001-4400m, 4401-5316m) using bootstrap samples. These distance classes were selected based on similar numbers of pairs of trees in each distance class for assessing patterns of synchrony with increased distance. I calculated the mean correlation ($\overline{r_s}$) and standard error for each distance class based on 5000 bootstrap iterations. For each iteration, correlations between pairs were chosen from the pool of all pairs such that each individual was only used once (Koenig & Knops 1998).

Within each distance class, I tested synchrony in cone production patterns between individuals against values selected to represent two dichotomies of synchrony. These dichotomies included 'no synchrony', if the mean correlation coefficient was not significantly greater than zero, and 'perfect synchrony', defined as counts over time for different individuals being piecewise parallel (Buonaccorsi et *al.* 2003), or the mean correlation coefficient was not significantly less than 1.0 (one-sided single sample t-tests and an alpha = 0.05). Although I conducted these baseline tests, I was less concerned with testing for statistically detectable synchrony, and was more interested in the levels of synchrony of cone production patterns with distance. This was because individuals may be statistically synchronous even if the mean correlation coefficient is very low (Koenig & Knops 2000).

SYNCHRONY IN MAST AND LOW CONE PRODUCTION YEARS

"Mast seeding" is defined as highly variable and synchronous production of seed crops by a population of plants (Kelly 1994), with "mast years" being those years when a heavy seed crop is produced (Norton & Kelly 1988). I was interested in synchrony of individuals in mast versus non-mast years, therefore I first defined mast years in the following the standardized deviate method in Chapter 3. This entailed expressing yearly cone production as the standardized deviate of the annual mean cone production of each plot to the long-term plot mean calculated over all years (i.e. (mean cones in year 't'– long-term mean cones) / SD calculated over all years). "Mast years" were defined as years in which annual cone production was both greater than the long-term mean and greater than the absolute magnitude of the variation below the mean. Years with cones close to the mean abundance will be close to 0 standardized deviates from the mean, low cone years will have standardized deviates that are negative, and high cone "mast years" will be positive and beyond the range of the negative standardized deviates. This approach uses the long-term variation in cone productivity occurring within a plot to dictate which years are mast years, as opposed to a theoretical distribution, allowing comparisons between sites having different productivity. Asynchrony between individuals could arise because different trees produce their largest cone crops in different years or because trees in mast years are highly synchronous but highly asynchronous in intervening years. I examined the synchrony of individuals producing their largest 'x' cone crops, where 'x' is the number of designated mast years (see above) at the plot level. The percentage of trees in each plot within each year producing one of their 'x' largest cone crops was calculated. Only trees in the data set for 13 to 16 years

were included in this analysis (n = 196). Synchrony in low cone production by individual trees was based on the percentage of trees within a plot that had their lowest cone production observed in a given year.

TEMPORAL PATTERNS OF INDIVIDUAL CONE PRODUCTION

Variation in synchrony of cone production among individuals may result from endogenous cycles within individuals. To examine this I calculated autocorrelation functions (ACF) for individuals in the data set for at least 13 years. Patterns of the dominant ACF lag for each tree were coded, from no significant lag to a maximum 5-year lag, and either positive or negative. Variation in the dominant cone production lag was analyzed with multinomial logistic regression and the modeling approach of Hosmer & Lemeshow (1989). Univariate multinomial logistic regressions were conducted with individual tree attributes of maximum basal area (cm^2) over the study and mean ln-transformed cone abundance. Both predictors had $P<0.2$, so were included in a multivariate model. If either term was non-significant ($P>0.05$) in the multivariate model it was removed in a stepwise procedure, until the remaining term were significant.

RESULTS

VARIABILITY IN CONE PRODUCTION

The annual mean number of cones per tree in a plot varied considerably over time (range: 0 to ~ 3200 cones), and the productivity of the plots was highly concordant over time (W = 0.80, $P<0.001$). Plot A typically had the highest cone production, followed by plots B, C and D (Figure 5-2). All four plots had their largest mean cone crop in 1998 but the

occurrence of mast years varied between plots. The two plots closest to each other, A and B (Figure 5-1), had 3 mast years (1993, 1998, 2005); plot C had 2 (1993, 1998); and plot D had 1 mast year (1998). While plots A and B produced a mast in 2005, plot C produced below average cones (mean = 87 cone per tree), and plot D had almost no cones (mean = 0.1 cones per tree). CV_p ranged from 1.31 to 2.74, with a significant positive autocorrelation at lag 3 for plots A and B; $\overline{CV}_i$ ranged from 1.84 to 2.15 (Table 1). Within a year, CV_A ranged from < 1 to > 6 among plots (Figure 5-3) and tended to be inversely related to annual cone production (r_s = -0.850, n = 60, $P < 0.001$).

SYNCHRONY IN CONE PRODUCTION

Pairs of trees over all distance classes were significantly correlated ($\overline{r_s} > 0$; all $P<0.001$), but all showed less than perfect synchrony (all $P<0.02$). The overall mean correlation coefficient was 0.52 ± 0.14 (mean ± SE), and levels of synchrony ranged from a high of 0.64 ± 0.18 for trees <75m apart, to a low of 0.33 ± 0.07 with >3 km between pairs of trees (Figure 5-4). There was no significant decrease in the average synchrony between pairs of individuals in from the closest to the farthest distance class (one sided *t*-test, t_{623} = 1.213, P = 0.113).

SYNCHRONY IN MAST AND LOW CONE PRODUCTION YEARS

In 1998, the year with the highest annual mean cones and when all plots produced a mast crop, 84-100% of the trees produced large cone crops (Figure 5-5). In 1993, 36-77% of the trees in plots A, B, and C produced large cone crops, and in 2005, 38 and 50% of trees in plots A and B produced one of their largest 3 cone crops. In years when the mean

cone production was relatively low 10-30% of trees within plots still produced one of their large cone crops. No trees produced a top cone crop in 1991 or 1994, when 65-95% of trees within plots did not produce cones. The percent of trees producing low cones varied substantially over time, with less variation between plots within a year. A notable exception was 2005 when plots A and B showed a mast year, while plot C had 50% and plot D >90% of trees producing low cones. In mast years on a plot, few trees failed to produce cones (on average 5.8%). There was only one complete cone failure observed (plot D in 2000). In the post-mast years of 1994 and 1999, 75-79% and 30-50% of trees in plots that masted the previous year, produced low cones respectively.

TEMPORAL PATTERNS OF INDIVIDUAL CONE PRODUCTION

Three patterns of temporal autocorrelation in cone production for individuals were commonly detected (Table 2). These included trees with no significant lag (86 of 196 trees or 44%), a negative correlation in cone production at one year (23%), or a positive correlation at 3-years (20%). Other lags included a negative correlation at 2 (6%) and 4 years (3%), and a positive correlation at 5 years (4%). There was no significant relationship between basal area and temporal patterns of cone production. Mean individual cone production influenced the lag patterns of cone production (Table 2); individuals with higher cone production were more likely to have a three-year lag, the same as that detected for two of the plots, compared to no significant lag (Table 2). Individuals with a negative 1-year autocorrelation produced fewer cones than individuals with no significant lag, although not significantly.

DISCUSSION

All of the *P. glauca* study plots exhibited mast seeding based on the high CV_p values documented (Liebhold et *al.* 2004). Overall, individual trees were moderately synchronous in their pattern of cone production with a mean correlation of 0.52, but this varied with distance between trees. This is in keeping with "moderate synchrony" used to describe mean Spearman and Pearson correlations of 0.53 previously (Buonaccorsi et *al.* 2001; Koenig et *al.* 2003, respectively). Individuals were highly synchronous at the most local spatial scale, and they showed low synchrony at distances over 3000m. My results suggest that mast years can vary in intensity. This can occur both through the variable occurrence of cone masts at the plot scale, and the levels of synchrony in the production of large cone crops by trees within plots during a mast year. The 1998 mast year produced the highest mean cone crop, and "masting" occurred over all study plots. In 1993, all but one of the plots masted, while in 2005 only half of the plots had a mast cone crop. The degree of synchrony within a year at the plot level appeared to vary with the magnitude of cone production. During the 1998 mast, synchrony in the production of large cone crops by individuals was especially high; only 10% of all trees sampled did not produce one of their large cone crops. In the other mast years (1993, 2005) the extent of masting was not as strong, with the percentage of trees within a masting plot that produced large cone crops varying from 36-75%.

Individual variation in cone production based on the annual CV_A was relatively low in mast years, and high in low cone years. Many trees produced large cone crops during mast years, as discussed above, increasing the mean relative to the variation among individuals in these years. However, in low cone years some individuals were

also producing large cone crops. Variation then seemed greater in low cone years, contributing to the high variation shown by the within year CV_A, and to the moderate level of overall synchrony. I found that variability in the number of cones produced among individuals within a year was inversely related to mean cone abundance within the year.

Analyses on 43 *Quercus* spp. acorn production datasets using mean Pearson correlation coefficients among individuals as measures of synchrony, ranged widely from 0.18 to 0.82 (Koenig et *al.* 2003). The mean Spearman correlation here was in the middle of this range at 0.52. Koenig et *al.* (1999) and Liebhold et *al.* (2004) studied synchrony in acorn production over small spatial scales (<10 km) and found little evidence for declines in synchrony with distance. Spatial synchrony in acorn production between individuals of three *Quercus* spp. based on Pearson correlations were in the range of 0.60 to 0.35 over distances up to 5km (Koenig et *al.* 1999). Although individual synchrony of one of their species (*Q. lobata*) tended to decline with distance, for *Quercus* spp. in their study there was either no statistically significant decline in mean synchrony of each distance class with distance, or it occurred at the scale of hundred's of kilometres. Although I found no statistical difference in the synchrony of *P. glauca* trees at 75m compared to 4km apart, synchrony did decline with distance to a low of 0.33. Whether synchrony in cone production by *P. glauca* individuals over larger distances declines further or not is still unknown. Only Koenig & Knops (1998) have examined this in *Picea* spp., but for population means; they found detectable levels of synchrony for population up to 2500km apart. Because I focused on the synchrony between individual plants and not population means, the overall mean correlation based on individuals was

lower than that based on means for populations less than 10km apart (0.73 here, ~0.70 from Koenig & Knops 1998). This suggests that considerable variation may remain undetected when population means are used in the analysis of synchrony and not individual values. This relates back to the need of studies focused on individuals to provide mechanistic explanations of the evolutionary phenomenon of mast seeding (Herrera 1998). Further analyses comparing levels of synchrony based on population means versus individuals will provide more insight in this regard.

Here, I reported that the correlation coefficients were statistically greater than zero at all distance classes, but I focused more on the patterns and relative amounts of synchrony among individuals rather than simply the statistical detection of synchrony. Previous studies have inferred synchrony from a statistically significant positive correlation among individuals (i.e. significantly > 0), regardless of how small and close to zero (Koenig & Knops 1998; e.g. a correlation of 0.12 ± 0.03 (95% C.I.); Crone & Lesica 2004). Further information on the amount of variability explained could be attained by squaring the correlation coefficients to generate 'correlation index' (r^2) values, representing the proportion of variability in the cone production pattern of a tree explained by correlating it with another tree (Zar 1999), while preserving the sign of the Spearman correlation. The correlation index may be useful for quantifying and interpreting the relative importance of correlations of different magnitudes compared to the correlation coefficient (r_s), especially when correlations are not very strong (not close to 1 or -1), nor very weak (not close to 0) (Sokal & Rohlf 1995).

With this approach, the mean proportion of variation explained in correlation index for the 356 trees was 0.35 ± 0.12. The spatial pattern of the proportion of

variability explained in cone production patterns between pairs of individuals had the same trend as the Spearman correlation, a decline with distance. The mean proportion of the variation explained ranged from a high of 0.47 ± 0.18 to a low of 0.21 ± 0.06 (see Appendix 1). Like the Spearman correlation for measuring synchrony, there was no significant difference in the mean correlation index between pairs of trees in the closest and furthest distance classes (one sided *t*-test, $t_{623} = 0.981$, $P = 0.164$). The variability in cone production patterns of trees explained by pairs of trees over all distance classes was statistically greater than 0, but there was still considerable variation in the cone production patterns of individual trees regardless of the scale tested.

Unexplained variation in synchrony among individuals could result from persistent individual differences in temporal cone production patterns. I detected three dominant patterns of cone production by trees. Some individuals showed no correlation in cone production over the years, each year is independent of those preceding it; others showed a significant negative effect of cone production in one year on the cones produced the next year; while other individuals, those producing more mean cones over the study than those in the other groups, displayed a positive autocorrelation at 3-year intervals. *P. glauca* cones develop over two years, with bud differentiation occurring in summer of one year and the cones produced the next year (Nienstadt & Zasada 1990); this is most consistent with the one-year lag in cone production. Greene & Johnson (2004) in a study of North American tree species reported 31% of the data sets in their study had significant lag 1-year autocorrelations, suggesting it was related to resource depletion; but provided no explanation for variation among trees. Local habitat quality (e.g. basal light availability) influences cone production (Greene et *al.* 2002), and energy

reserve dynamics of individuals could affect their seed production patterns (Satake & Iwasa 2000). In high quality areas trees may have more resources, resulting in both high cone production within a year and allowing trees to produce cones over successive years (Nienstaedt & Teich 1972) and in a multi-year lag in cone production. Kelly & Sork (2002) predicted that high quality areas should also have lower variability in seed crops (lower CV_p among years) due to higher mean seed production; this was displayed by the plots examined here. Habitat variability within sites could be a factor in the variation in synchrony in *Quercus* spp. mentioned previously (Liebhold et *al.* 2004). A tendency for a small proportion of trees to produce a large proportion of seed in a population has been shown in *Quercus* spp. (Healy et *al.* 1999). A similar pattern of a minority of trees producing the majority of cones has been observed in our data (LaMontagne & Boutin, unpublished data); and the trees that produced more mean cones over the study had a dominant 3-year lag in cone production. The dominant lag for the high mean cone producing trees coincided with the significant plot-level lag in cone production (3-years) for two plots. If the cone-production ability of individuals is related to local site conditions, then relatively homogenous areas could have higher synchrony among individuals compared to an area where there is a significant amount of local site variability.

WEATHER AS A CUE FOR SYNCHRONY

It has been suggested that broad scale weather acts as a cue ensuring the majority of trees are synchronous seed producers (Norton & Kelly 1988). Koenig et *al.* (1999) proposed that the synchronizing effect of weather over large areas, known as the Moran effect

(Moran 1953), could be responsible for synchrony in acorn production by Quercus spp. over hundreds of kilometres. Schauber et *al.* (2002) found that abnormally high temperature in the summer before seedfall, consistent with the La Niña phase of the El Niño Southern Oscillation, was associated with synchronous fruiting in multiple species across New Zealand. Bud development in many conifer species occurs a year prior to cone formation, triggered by hot dry conditions during the period of differentiation into vegetative or sexual buds (Owens & Molder 1977; Nienstaedt & Zasada 1990; Selås et *al.* 2002). Detectable levels of synchrony in spruce seeding occur over large spatial scales (Koenig & Knops 1998). Here, trees at the furthest distance classes, 3 to 5.3km, had ~30% of their variability in cone production patterns accounted for by correlating it with another tree in these distance classes. However, in mast years, within a plot most individuals produced their largest cone crops in synchrony, and all plots had a mast in 1998. In addition, all mast years either occurred in 1993, 1998, or 2005; no mast years occurred outside these years perhaps because the large-scale cue was not present.

Janzen (1971) postulated that for weather to be a synchronizing factor over a large area that it must be of a sufficient intensity to override differences due to local conditions. This could be the case here. Over the relatively small spatial extent of my study area I expected that the general climatic conditions of temperature and moisture that favour the formation of reproductive buds, namely being hot and dry during late July (Neinstadt & Zasada 1990), would not differ. However, tree growth and seed output are also affected by soil moisture and competition for resources (Greene et *al.* 2002), and therefore should be correlated for individuals close together, leading to patterns of local high synchrony. Perhaps local microsite conditions were such that if the action of weather synchronization

has to achieve some threshold to override local variation, that conditions leading up to the 1998 mast year were perhaps well above this threshold so all areas had a cone mast, whereas 1993 and 2005 were nearer the threshold such that some plots were below while others were above. Or, that local moisture or frost conditions during the very short time of pollen shedding (3 to 5 days; Nienstaedt & Zasada 1990) negatively affected further synchronised masting. I did not have climatological data to pursue this further. The spatial variation in mast years, and variability in individual synchrony could reflect the variation in habitat conditions (Liebhold et *al.* 2004) when these conditions are not overridden by weather for mast seeding. The broad scale patterns of some detectable level of synchrony in population means observed over very large distances (e.g. Koenig & Knops 1998) could result from large scale climatic conditions that trigger a mast year across sites over large distances, with considerable variation in the other years.

POLLINATION EFFICIENCY AND PREDATOR SATIATION

It was not my goal to differentiate between evolutionary hypotheses for seed masts, so I will only briefly comment on pollination efficiency and predator satiation in light of my results on variability and synchrony. The high CV_p and $\overline{CV_i}$, along with high local $\overline{r_s}$ could be the response to selection due to local pollination efficiency and localized seed predators (Koenig et *al.* 2003). *Picea glauca* pollen is wind dispersed; pollen from wind dispersed conifers often follows a leptokurtic distribution, with the majority of pollen falling close to the source tree, and a low-frequency of successful pollination occurring over long distances (Robledo-Arnuncio & Gil 2005). This pattern of pollen dispersal could be a reason for individuals being more highly synchronous when closer

together, and could reinforce via heritability the different patterns of lags observed in cone production that could reflect different strategies or abilities. Genetics may also play a role in the mast seeding behaviour of *P. glauca* individuals, but I do not have the data to test this idea further. In addition, the seed production in successive years that occurred for individuals in this study, is not disadvantageous based on the pollination efficiency hypothesis (Norton & Kelly 1988).

On the contrary, cone production patterns evolving for predator satiation should select strongly against reproduction in successive years, because high predator levels following the first year would lead to heavy seed losses in the second (Janzen 1971; McKone & Lloyd, in Norton & Kelly 1988). I documented 23% of the trees in my study had a negative relationship between cone production in successive years. Consequently, as the only conifer species in my study area, individual *P. glauca* should experience strong selection to be synchronous due to predation pressure. However, this selection is likely influenced by the attributes of predator species. Red squirrels are territorial thus do not roam in search of food resources, unlike birds such as crossbills (Holimon et *al.* 1998). If the dominant seed predator had high mobility then very high synchrony in seed production may occur over the range of the seed predator. Red squirrels feed on *P. glauca* seed as a primary food source (Smith 1968) and individuals cache upwards of 12000 cones prior to seed fall (Hurly & Lourie 1997), preferentially selecting cones from trees with larger cone crops (Peters et *al.* 2003). In addition, seeds lose their viability after 1-2 years in a red squirrel cache (Nienstadt & Zasada 1990). Therefore selection should act against trees producing asynchronous large cone crops with other trees, but this may only be important in a local area, within a red squirrel territory (0.25ha, or a

diameter of about 60m; LaMontagne & Boutin, unpublished data). Selection at this scale may contribute to the high level of synchrony among individuals in the closest proximity (<75m).

Synchrony was lower with increased distance between trees, implying there are areas where trees produce many cones when other trees produce small cone crops. This asynchrony may promote seed predator persistence, such as red squirrels, especially in low seed years. However, mobile generalist seed predators may show the opposite of predator satiation (i.e. higher proportion of the seed crop consumed in high seed years or for high-seed trees), as shown for *Betula allegheniensis* (Kelly et *al.* 2001). Under these conditions it might be more favourable for individual plants to be highly variable (high $\overline{CV_i}$) with lower spatial synchrony to tailor the amount of variation and its spatial scale to the characteristics of its seed predator(s), as outlined by Koenig et *al.* (2003).

I suggest that variation in the levels of synchrony in seed production should be expected. Different species and even different populations of a common species will experience different selection pressures via the characteristics of seed predator populations, developmental times (e.g. promoting asynchrony between different species of *Quercus* spp. in a common area; Liebhold et *al.* 2004), and local environmental variation. Based on high synchrony locally, high synchrony within a mast year, and multiple lags in cone production by individuals, both available resources and strong weather cues appear to play roles in the observed patterns. Spatial variation in the occurrence of mast years can have an affect on the population dynamics of seed predators and local community dynamics (Ostfeld & Keesing 2000). There is much opportunity to

further investigate variation in synchrony and determinants of individual lags in seed production, to understand seeding patterns within plant populations.

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Table 5-1: Number of years of data for each of the study plots (n), and for each plot, the coefficient of variation (CV_p), the mean spearman correlation for synchrony of pairs of trees ($\overline{r_s}$), the mean CV for individuals in each plot ($\overline{CV_i}$), and the autocorrelation function value (ACF_t; 't' represents the lag in years) and standard error. The maximum ACF lag calculated was approximately three times shorter than the data series. See text for number of individuals in plots.

Plot	n	CV_p	$\overline{r_s}$	$\overline{CV_i}$	ACF_1 (SE)	ACF_2 (SE)	ACF_3 (SE)	ACF_4 (SE)	ACF_5 (SE)
A	16	1.31	0.59	1.84	-0.400 (0.230)	-0.380 (0.226)	0.544 (0.217)*	-0.219 (0.208)	-0.164 (0.198)
B	16	1.40	0.59	2.07	-0.447 (0.234)	-0.317 (0.226)	0.551 (0.217)*	-0.341 (0.208)	0.023 (0.198)
C	15	1.71	0.50	2.10	-0.371 (0.241)	-0.337 (0.231)	0.316 (0.221)	-0.102 (0.211)	-0.069 (0.200)
D	13	2.74	0.63	2.15	0.151 (0.251)	-0.275 (0.221)	-0.209 (0.187)	-0.217 (0.167)	

*$P < 0.05$

Table 5-2: Final model from multinomial logistic regression for dominant ACF lags. Individual trees with a negative lag at 1 year, or a positive lag at 3 years were compared to trees with no significant lag. 'n' is the number of individuals with each pattern. Trees with dominant lags of 2, 4 and 5 years were omitted from this analysis; they comprised only 10% of individuals sampled.

ACF_t	n	Parameter	*b* (se)	*P*	Odds-ratio (95% CI)	Mean log(cones) (se)	Mean basal area cm^2 (se)
No lag significant	86					2.46 (0.13)	246.7 (20.2)
Lag 1 negative	46	Intercept	-0.112 (0.390)	0.774			
		Mean ln(cones)	-0.224 (0.153)	0.143	0.799 (0.592, 1.079)	2.13 (0.18)	194.6 (23.8)
Lag 3 positive	40	Intercept	-2.329 (0.552)	<0.001			
		Mean ln(cones)	0.548 (0.171)	0.001	1.729 (1.235, 2.420)	3.24 (0.18)	283.4 (30.1)

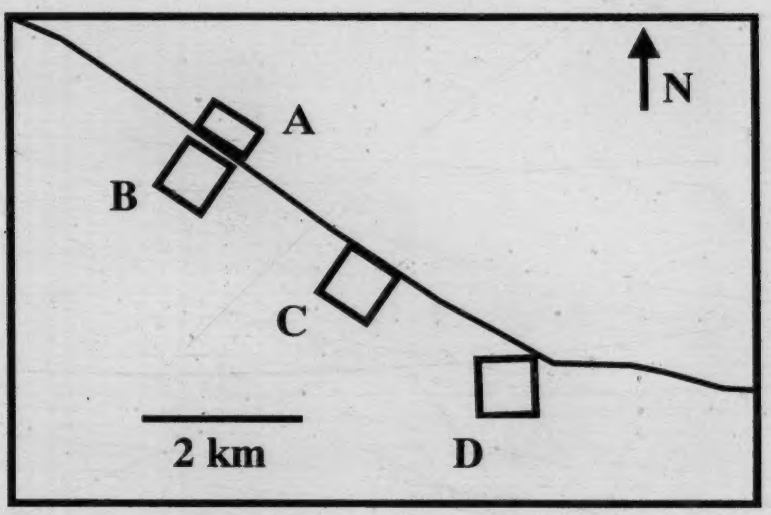

Figure 5-1: Study plot locations for *P. glauca* synchrony in cone production, Yukon, Canada (61°N, 138°W). The line in the map represents the Alaska Highway.

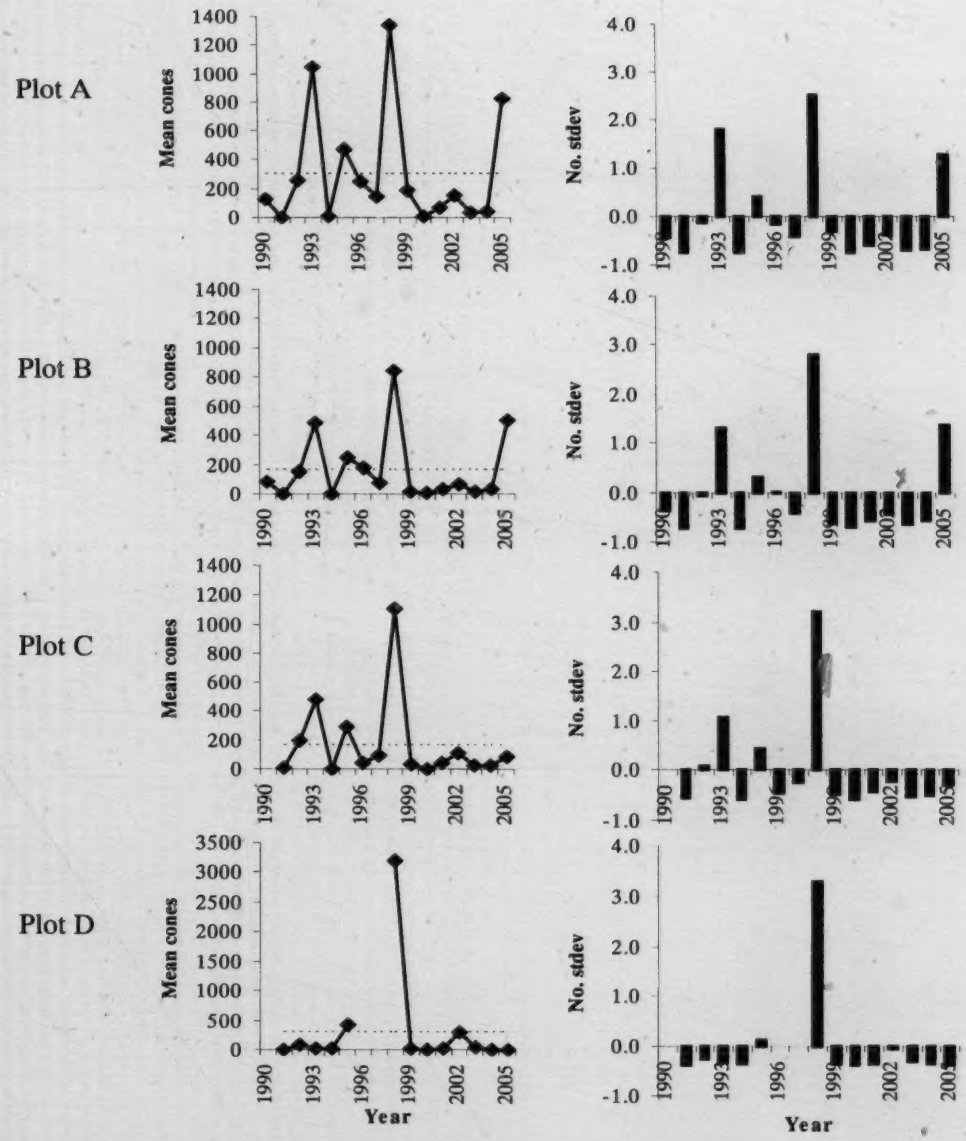

Figure 5-2: Mean annual *P. glauca* cone production for each study plot from 1990 (or 1991) to 2005 in the Yukon, Canada (left panels). The dashed line is the long-term mean cone production. Right panels show the number of standardized deviations the annual cone production mean was from the long-term mean. Filled symbols/bars represent mast years based on deviations in cone production from the long-term mean (see methods).

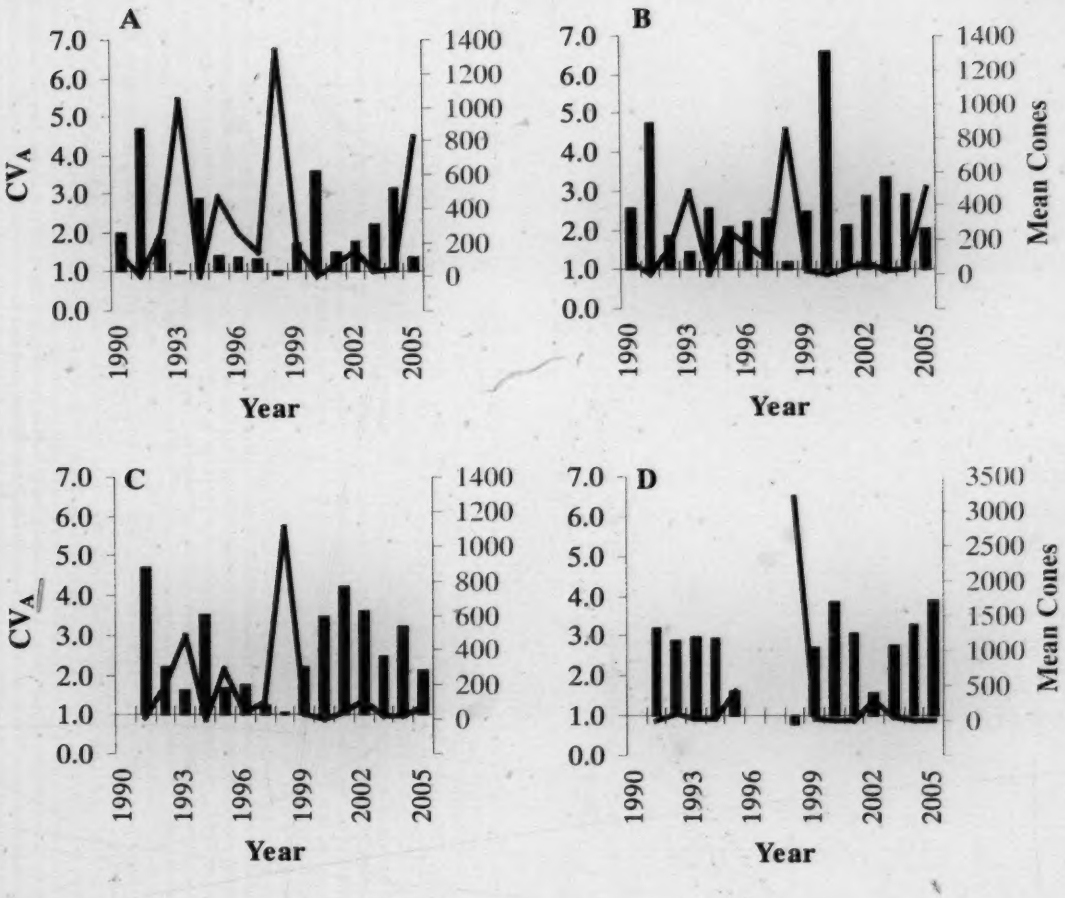

Figure 5-3: Within-year coefficient of variation (CV_A; bars) with mean annual cone production (line), for each of the study plots: A (n = 83), B (n = 84), C (n = 84), and D (n = 105) from 1990 - 2005.

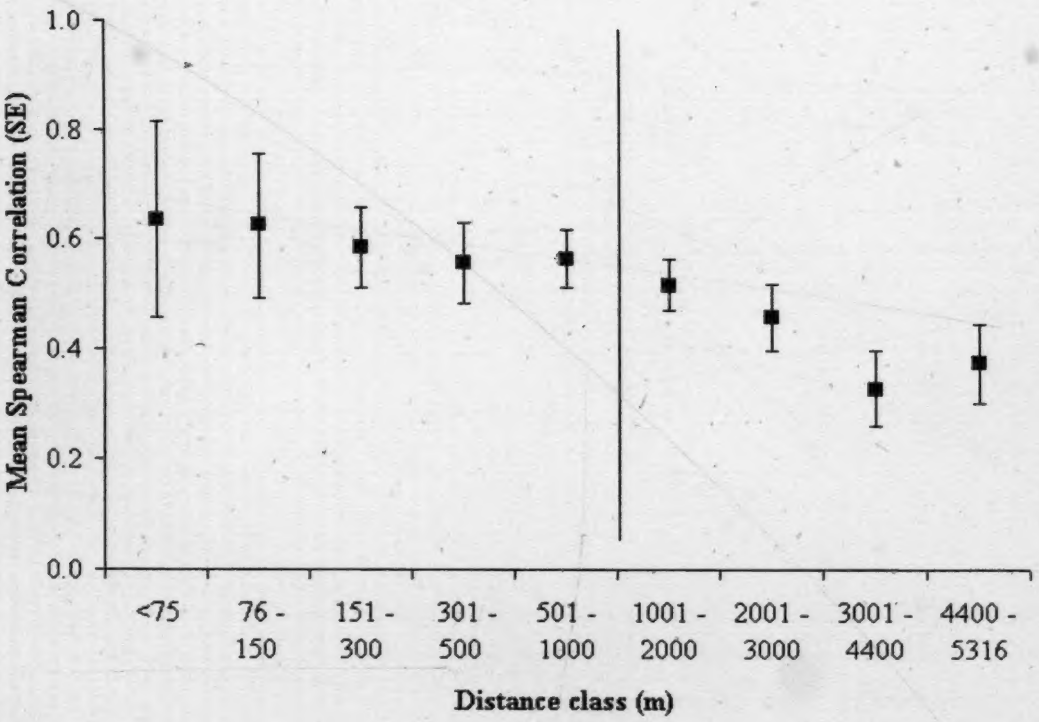

Figure 5-4: Spatial variation in synchrony of cone production by *P. glauca* pairs of individuals. The vertical line is where distances between tree pairs generally move from within to between study plots. All mean correlations for each distance class were significantly greater than zero and less than one.

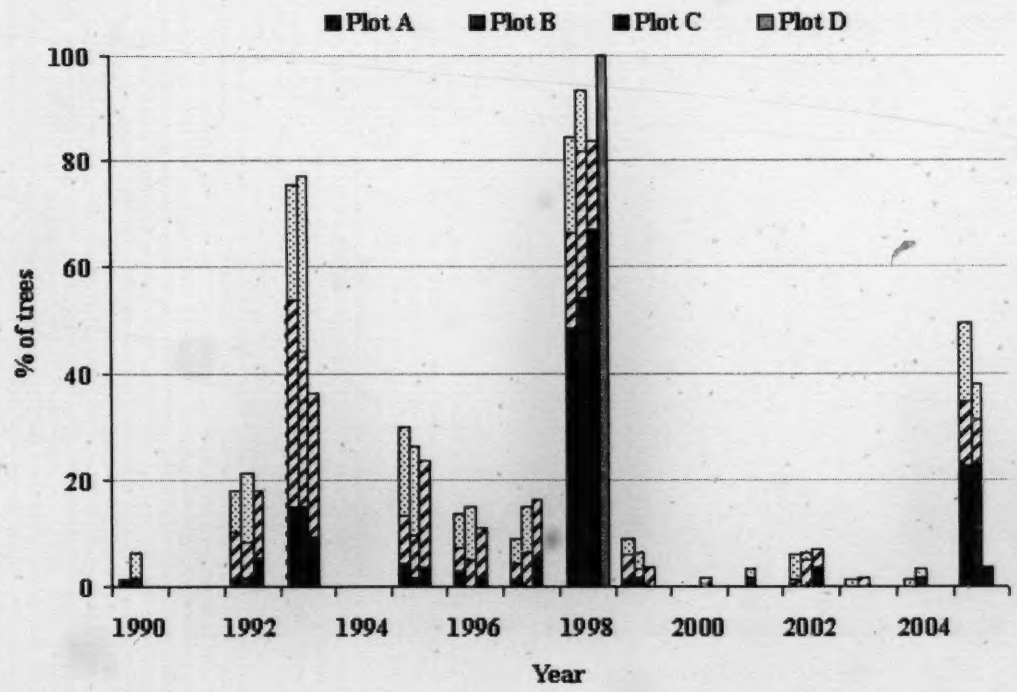

Figure 5-5: Percentage of *P. glauca* trees that produced large cone crops within each year. Only trees in the data set for at least 13 years were included in analysis. Large cone crops were defined as the number of mast years that occurred at the plot scale (see Figure 5-2). Plot A (n = 66) and B (n = 61) have their top 3, plot C (n = 55) has its top 2, and plot D (n = 14) has the single top cone year shown. Solid bars represent the top cone year, angled lines represent the year with the second highest number of cones, and dotted bars represent years with the third most cones, when shown. Recall that data for plots C and D span 1991-2005 only, and no data are available for plot D in 1996 and 1997.

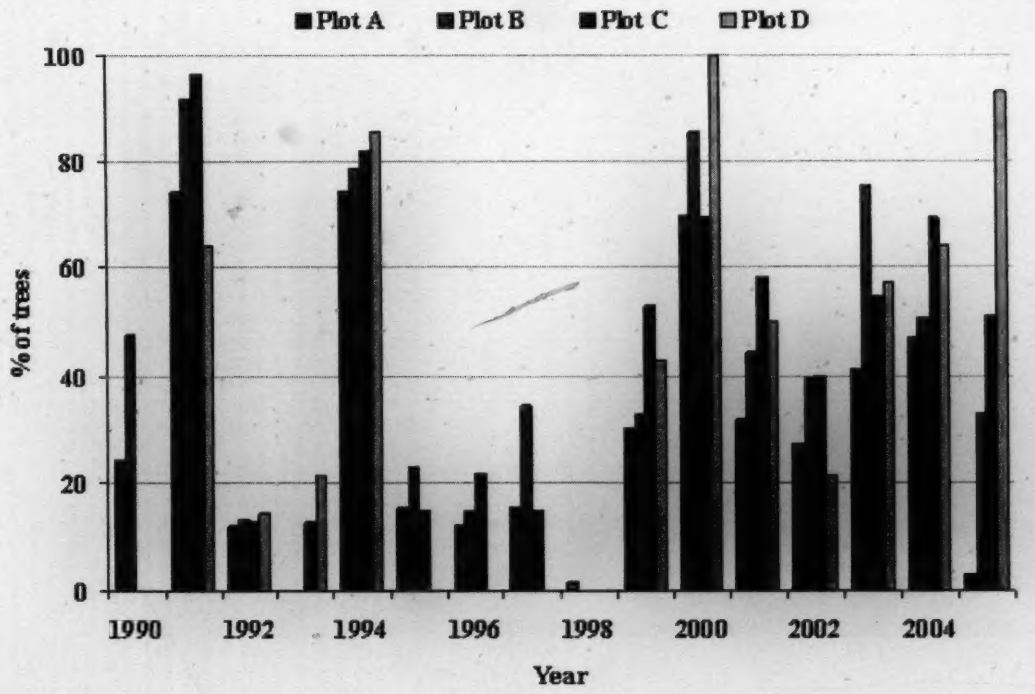

Figure 5-6: Percentage of *P. glauca* trees producing their lowest cone crop within each year for each of the four study plots. Only trees in the dataset for a minimum of 13 years were included in the analysis. The lowest cones may occur in more than one year for each tree. Sample sizes are the same as in Figure 5-5. Recall that Plots C and D span 1991-2005 only, and no data was available for plot D in 1996 and 1997.

CHAPTER 6

INTRASPECIFIC VARIATION IN TERRITORY SIZE, TERRITORY QUALITY, & THEIR EFFECTS ON INDIVIDUAL PERFORMANCE IN RED SQUIRRELS

INTRODUCTION

Territory size varies among individuals within populations, both between and within habitats (Wiens 1973; Gill & Wolf 1975; Wiens et *al.* 1975; Kodric-Brown & Brown 1978; Boutin 1990; Steury & Murray 2003). To explain this variation, researchers have investigated factors that may influence territory size. For food-based territories, territory size may vary inversely with food density (Kodric-Brown & Brown 1978; Keeley 2000), such that across habitats all territories contain similar amounts of food and individuals have equal fitness (Fretwell & Lucas 1970). Or, in temporally variable environments, territories may be larger than required to meet energetic demands when resources are abundant if territory size is set by energetic requirements during food shortages (Myers et *al.* 1979). Consequently, there could be no relationship with resource availability, or larger territories could contain more resources. The former could also occur because a territory provides resources in addition to food (e.g., nest sites, refuge), individuals cannot assess available food, or neighbours resist territory expansion (Mares et *al.* 1982; McNair 1987; Adams 2001). In addition to local food density and conspecific density, age, mass, and sex of the territory owner (Hixon 1980; Keeley 2000; Steury & Murray 2003) may influence territory size.

In natural populations it is often assumed that food resources within a habitat are distributed homogeneously, such that individuals with larger territories have greater access to food (e.g., Steury & Murray 2003). In this situation, relative territory size may

be a good surrogate measure of relative food levels in a territory. However, all landscapes are heterogeneous at some spatial scale (Wiens 2000), and territory size may not be equivalent to territory food levels. Habitat composition of territories has been used to assess territory quality and then associated with individual performance (survival, reproduction) (Ferrer & Bisson 2003; Kerbiriou et *al.* 2006). Less is known about the relationship between an individual's territory size and territory food levels, *within* a habitat-type, and how they affect components of their fitness (survival, reproduction). Without information on resource levels within territories the ecological significance of variation in territory size among individuals cannot be evaluated (Wiens et *al.* 1985). Food supplementation experiments have shown food availability can affect territory size, life-history traits of individuals, and population demography (see Boutin 1990, Adams 2001). The inability to quantify food availability to individuals within a natural population has been a limitation in linking territory quality to variation in individual performance (Wiens 1984; Łomnicki 1988; Boutin 1990).

Individuals of many species store food to ensure a steady energy supply through periods of low food availability in temporally variable environments (Morse 1980; Vander Wall 1990). Temporal variation in food availability includes late summer peaks in seed, nuts, or green vegetation that are followed by the winter season when food resources are scarce. Individuals may store food in a concentrated area (larder hoards; Vander Wall 1990) when they can defend their cache from competitors (Smith & Reichman 1984). Individual territoriality in the genus *Tamiasciurus* is thought to be based on defending caches of seed (C. Smith 1968; Smith 1981). Seeds are often produced with high temporal and spatial variability (Greene & Johnson 1994; Greenberg

2000; Greene et *al.* 2002; Kelly & Sork 2002; Fenner & Thompson 2005; Chapters 3 & 5). If food availability is highly temporally variable, the size of a profitable territory in one year may not be profitable in other years.

Red squirrels (*Tamiasciurus hudsonicus*) are a good species to study links between territory size and territory resource levels, factors affecting territory size and territory quality, and how both these territory attributes impact individual performance. Red squirrels are aggressively territorial, vocally conspicuous, readily habituate to human observation (Vlasman & Fryxell 2002), and they occupy individual, non-overlapping territories year-round (Gurnell 1984). In the boreal forest, red squirrels rely heavily on conifer seeds, and a territory with a central cache of cones (a midden) is considered essential for overwinter survival (C. Smith 1968; Steele 1998). Individuals rarely change the location of their territory (C. Smith 1968; Price et *al.* 1986; Larsen & Boutin 1995). Based on their high reliance on conifer seed, I defined an individual territory's food level, or quality, as the estimated number of white spruce cones contained within the territory.

Results of previous studies on red squirrel territory size have ranged from a constant territory size with natural temporal fluctuations in food (Rusch & Reeder 1978) to an inverse relationship of territory size with local food availability (C. Smith 1968). In a food supplementation experiment conducted in two habitat types, Klenner (1990) found a negative relationship of red squirrel territory size with increased food in one habitat (Douglas fir, *Pseudotsuga menziesii*) and no effect of food supplementation in the other (white spruce; *Picea glauca*). Recently, Steury & Murray (2003) suggested that larger territories within a habitat type contained more food than smaller territories. To examine the relative importance of territory size on individual performance, information on food

levels within territories is needed. Here, I investigate the effect of natural spatial and temporal variation in food availability on the relationship between territory size and territory food levels, examine determinants of individual territory sizes and territory food levels, and assess their effects on individual performance. This includes quantifying the availability of the primary food resource of red squirrels, conifer cones, within each territory. I test the hypotheses that 1) territory size is dictated by local food availability, or, that 2) territory size and territory food levels are a function of the attributes of the territory owner, of the local habitat, and population density. I also test the hypothesis that 3) territory size and/or food levels are significantly related to an individual's performance, specifically their ability to survive overwinter and (for females) their reproductive success the following year.

If red squirrels adjust their territory size based on local cone density to have access to constant food levels across individuals, then territory size and local food density within the territory should be inversely related. An adjustment by individuals for local food availability would result in there being no relationship between territory size and the total food level in a territory. However, if food levels vary across territories, I predict that an individual's territory food level should be a better predictor of overwinter survival and reproductive success than territory size. Should survivorship and reproductive success not vary as a function of food-levels, but rather correlate with territory size, this would indicate that territory size confers other benefits to individuals beyond seed resources alone.

METHODS

STUDY AREA

Red squirrels and their white spruce seed resource were studied on 36 ha and 26.5 ha study plots in the south-western Yukon, Canada (61°N, 138°W) from 2002 to 2005. The vegetation is dominated by white spruce, the only conifer species in the area, with some trembling aspen (*Populus tremuloides*), and a shrub understory dominated by grey willow (*Salix glauca*). In this area, white spruce has years of complete cone failure, when virtually all trees produce zero cones, years of low-intermediate cone production, and mast years (Dale et *al.* 2001; Chapter 3). Precipitation is low (annual mean = 230 mm) falling primarily as rain during the summer months; mean snowfall is 100 cm (Turkington et *al.* 1998). Grid stakes had previously been established throughout each study plot at 15 m to 30 m intervals, and facilitated identifying locations for territory mapping and placement of cone count stations (see below).

All squirrels were uniquely ear-tagged and marked with coloured wires, and the sex, age, and mass of all squirrels within the populations were known. Biannual population censuses were conducted in May and August. In spring, all females were trapped regularly and assessed for pregnancy. Females were monitored for litter size, the number of juveniles emerged, and the number weaned. During summer the mass of individual red squirrels was monitored at least biweekly using a Pesola scale. See Humphries & Boutin (2000) for more information on trapping. Only some causes of mortality were known (e.g., predation (inferred from finding a radiocollar plus fur or tail), versus a body found, not predated). Individuals were considered to have not survived overwinter if they did not appear in the following May census. This was

because few red squirrels change the location of their territory once they become established (C. Smith 1968; Price et *al.* 1986; Larsen & Boutin 1995).

TERRITORY MAPPING

I mapped territories of a sample of primary midden owners during late-July to early August, in each of 2002 to 2004, regardless of the age and sex of the midden owner. A primary midden is the main active cone cache in an individual's territory, a feature composed of fresh cone bracts and tunnels where cones are stored (Gurnell 1984). My original goal was to map nonadjacent animals based on a sample of primary middens selected in 2002; this was not always possible due to low population densities (as low as 1.49 individuals · ha^{-1} in 2004). If a primary midden owner died, I mapped the new owner, regardless of whether the midden remained a primary midden or not. If an owner was unknown at the beginning of the mapping period, I mapped one or more neighbouring midden owners. If a female gave part or all of her territory to one or more juveniles (based on the May population census (Boutin data) and June territory mapping (not shown here)), both the female and her juvenile(s) on her territory were mapped.

I determined fall territory boundaries for individual red squirrels at least two weeks after a female's offspring had weaned, in late-July and August, when juveniles were expected to have settled a territory. For males and nonbreeding females, I mapped their territories at least two weeks after nearby breeding females had weaned their offspring. I assumed adult and juvenile territories would remain constant during caching (mid-August to mid-October; LaMontagne, pers. obs.; Humphries et *al.* unpublished data). Individual territories were mapped for up to two to three weeks using a

combination of radio-telemetry and direct observations (Price et *al.* 1986; Larsen & Boutin 1994), and recording grid locations and behaviours. I converted all grid locations to Universal Transverse Mercator (UTM) locations in ArcView 3.2 (ShapeWarp; McVay 1988) based on reference locations within the study site. I used locations of at least 17 territorial behaviours, including territorial calling (rattles), caching, chasing another squirrel, scent marking, and eating in a tree, to calculate 100% minimum convex polygons (100% MCPs) of each territory (Vlasman & Fryxell 2002; Appendix 5) using Hawth's tools in ArcGIS 9.0 (Beyer 2004).

QUANTIFYING CONE AVAILABILITY

I collected information on the distribution of tree basal area and cones per unit basal area to map the distribution of white spruce cones in the study area in 2002 to 2005.

White spruce basal area distribution

I collected data on white spruce density and basal area by placing three 4m x 25m quadrats at 60m intervals across each study plot at established grid stakes at directions of 0°, 120°, and 240° from the stake. In 2002, I counted and measured the diameter at breast height (dbh) of all white spruce >5 cm (capable of producing cones, LaMontagne & Boutin unpublished data) within a quadrat. I assessed the spruce beetle status (currently attacked, attacked previous year, dead; Garbutt 2002) of each tree because a spruce beetle infestation was present in the area beginning in 1994 and increased in intensity again starting in 2002 (Garbutt 2002; Pretzlaw et *al.* 2006). In 2004, I assessed the spruce beetle attack status of all trees in transects again; attacked and dead trees were

counted and their dbh measured. I calculated the basal area of all live healthy trees within the each quadrat assuming trees were round.

I converted the total basal area of live spruce within each quadrat to a density (per $10m^2$), and centred this value in the quadrat, 12.5 m from the grid stake location in ArcView 3.2 (Jenness 2003). I determined trees alive in 2003 by adding the basal area density of newly killed trees in 2004 from the total number of live trees in 2004. I estimated the density of live trees in 2005 by subtracting the number of attacked trees in 2004 from the live trees in 2004 (similar to Pretzlaw et *al.* 2006). For each year I created a map of white spruce basal area density. I used basal area because it has been known to explain a significant amount of the variation in white spruce cone production (Greene et *al.* 2002; Appendix 6). I performed ordinary kriging (Isaaks & Srivastava 1989), an interpolation method that uses data observed at known locations to predict unknown values, using the 558 sampling locations (186 stakes x 3 quadrats). The fit was based on an exponential semivariogram with information from the neighbouring 8 stakes (to distances of about 110 m) in ArcGIS 9.0 to create the distribution of white spruce basal area density for 2002 to 2005, using a cell size of $10m^2$.

White spruce cone production

I quantified annual spatial variation in white spruce cone production by counting cones on trees at 60m intervals in each of 2002 to 2005. The three trees >5 cm dbh closest to the grid stake were selected for cone counts (n = 513 trees per year). If a tree died during the study it was replaced with the next closest appropriate tree. I recorded the distance and direction (in degrees) of each tree from the grid stake. An observer

standing on the ground, using binoculars, counted all visible cones in the top 3 m of the crown, from one side of the tree. New cones produced by trees are easily identified because white spruce trees produce new green or purple cones in mid-summer, opening in fall to release seeds and the empty cones typically fall from the trees during winter (LaMontagne et *al.* 2005; Chapter 2). If >100 cones were visible, a photograph was taken and the cones later counted. Visible cones were converted to total cones: Total cones = $10^{(0.073 + 1.189 \cdot \log(\text{visible cones}))}$ (LaMontagne et *al.* 2005; Chapter 2). Cones were counted in late July or early August, prior to caching by red squirrels (Peters et *al.* 2003). I calculated the number of cones per unit basal area (cm^2) for each tree and placed this value in the actual UTM location of the tree based on the distance and direction from the stake (Jenness 2003). This was done separately for each year.

I created a map of the spatial distribution of cones per cm^2 of basal area for each year using Inverse Distance Weighting (IDW) with a power of 1 (optimized in ArcGIS 9.0) and a distance of ~90m. I used this method because IDW was a better fit to the spatial variation in cone production than a kriged surface that smoothed out much of the variation (not shown). Also, cone production is expected to be more similar among trees locally (LaMontagne & Boutin, in review: Chapter 5). Although basal area may explain a significant amount of the variation in white spruce cone production, additional variation due to microclimatic conditions may also affect cone production (Greene et *al.* 2002; see Appendix 6). I created maps of the annual distribution of cones within the study area by multiplying the annual distribution of live white spruce basal area and the cone production per unit basal area using the raster calculator feature of ArcGIS 9.0. I

included the spatial distribution for 2005 to demonstrate variability in cone production during a mast year, even though data on territory size was not available.

TERRITORY FOOD LEVELS

Within an individuals' territory I obtained the total number of white spruce cones in fall of the year, and the basal area of live trees using Zonal Statistics in Hawth's Tools (Beyer 2004). For each territory 100% MCP, this tool summarized the total number of cones and total basal area of live trees in the annual spatial distribution maps that fell within the bounds of each territory polygon. I also calculated the number and total basal area of live white spruce trees (in cm^2), and the total number of cones in an area surrounding the primary midden equal to the minimum mean historical territory size of 0.1ha (Chapter 4) from each of the 2002 to 2004 kriged layers using Zonal Statistics. This information was used to determine if individuals adjusted their territory size to local food abundance around their midden, and to examine how local food abundance affected the total amount of cones within the extent of an individual territory. I refer to these as local cone production, or local tree or local basal area densities. Additionally, if territory size or the total amount of cones in a territory were related to these local measures of food conditions around the midden, they may be used to estimate the territory size and territory cone levels available to other individuals in the population.

ANALYSIS

I assessed the relationship between territory size and the number of cones in a territory, over all years and for each year separately using Spearman correlations, because the data

were not bivariate normally distributed (Zar 1999). I compared the slopes of the relationship between territory size and territory cones among years, and conducted Spearman correlations between territory size and the total basal area of white spruce within the territory.

Determinants of territory size & territory cone levels

I used a manual backwards-stepwise linear regression based on AIC_c to test the influence of individual red squirrel characteristics, local habitat attributes, and population density on pre-caching (August) territory sizes (ln-transformed). Individual attributes included the age-class (adult or juvenile), sex, minimum August mass (in g), and the number of offspring weaned during the year by the territory owner. I included the number of offspring weaned because females may give part of her territory to her offspring (C. Smith 1968; Berteaux & Boutin 2000), affecting her resulting territory size. Zero offspring weaned represented nonbreeding females, failed breeders, juveniles, and males. Local habitat characteristics in a 0.1ha area surrounding the primary midden included the total basal area of white spruce of cone production size (>5cm dbh), and ln-transformed local cone production. Interactions between age-class and mass, mass and population density, and mass and local cone production were also considered. These interactions with mass were included because within an age-class or for a given population density, a larger individual may have an advantage over smaller individuals. In addition, a larger individual may be better capable of compensating for local cone conditions such that a larger individual in a poor quality area may have a comparably larger or more cone rich territory than smaller, and potentially less competitive,

individuals. Prior to modelling, I examined the correlations between all independent variables, including age (in years) and local (0.1ha) tree density. Age was correlated with mass ($r_{spearman} = 0.788$), and local tree density correlated with local basal area density in 0.1ha ($r_s = 0.894$), so I excluded age and local tree density from further analyses.

The modeling approach started with a full model and I manually removed parameters based on minimizing AIC_c at each step (Hongzhi & Lan 1989). The manual stepwise technique allowed interaction terms and single-term main-effects models to be considered, while the total number of models was reduced drastically in producing the final model (Shtatland et *al.* 2001) from 256 potential models. To compare the model fits relative to the number of parameters, I compared the models at each step and models with main effects only using AIC_c weights (Burnham & Anderson 1998). I used this same approach, including the same parameters, to evaluate factors influencing the total number of cones contained within territories. Prior to regression analyses, I tested both territory size and the total number of cones in the territories for intraclass correlation based on focal middens. Data for both territory size and territory resource levels were considered independent (both correlations < 0.05). However, some of the dependent variables had significant intraclass correlations within focal middens, so I clustered based on the focal midden during model fitting to adjust the standard error of estimates.

Territory size, food resources, and individual performance

I conducted univariate and bivariate logistic regressions to separate individuals that survived overwinter (to the May midden census) based on territory size and the number of cones within a territory from individuals that did not survive. No other factors

were included since they had been included in the models of both territory size and number of cones in the territories. I assumed that the energetic requirements of adults and juveniles for overwinter survival were similar. The body size of adults is larger (251.6 ± 2.5 g) than juveniles (201.3 ± 4.9 g; August masses) with higher energetic demands (Humphries et *al.* 2005). However, juveniles surviving overwinter gain mass (mean of 47.0 ± 4.4 g from August to May, 2002 to 2005, n = 41; Boutin, unpublished data) that would require more energy than if they only maintained their smaller body size.

For the adult females (from fall) that survived overwinter, I used logistic regression to separate reproductively successful females from those that were not successful. I examined female reproductive success for three different stages including: i) females that produced a litter the following spring or not, ii) females with at least one offspring successfully emerged from the nest or not, and iii) those females with at least one offspring successfully weaned or not. Yearling females were not included in the above analysis because female red squirrels do not consistently breed at one-year of age (Rusch & Reeder 1978); they are typically two-years old at first breeding (Becker 1993). I used AIC_c and area under the curve estimates from receiver operating characteristic (ROC) curves to compare model performance (Hurvich & Tsai 1989; Hosmer & Lemeshow 2000). ROC values of 0.5 suggest no discrimination between groups; values between 0.7 and 0.8 represent acceptable model accuracy, and above 0.8 represent excellent discrimination (Hosmer & Lemeshow 2000).

Following each model fit, I determined the optimal probability cutoff points for classification purposes based on maximizing both sensitivity and specificity (Hosmer & Lemeshow 2000). I pooled all years for analyses; assuming that individual requirements

for overwinter survival and reproduction did not change significantly between years. During this study there was no significant difference detected in the monthly means of daily minimum temperatures over the coldest part of winter (November to March) among years based on weather data from the town of Haines Junction located 40km away (Environment Canada website (ANOVA, $F_{2,12} = 0.57$, $P = 0.578$). Means ± standard errors are reported, unless otherwise indicated.

RESULTS

I generated 93 pre-caching territory maps (100% MCPs) between 2002 and 2004 based on 3374 territory locations (mean = 36 ± 10 locations per territory). Twenty-one individuals were mapped in 2002 (14 adult females, 6 adult males, 1 juvenile), 32 in 2003 (14 adult females, 13 adult males, 5 juveniles), and 40 in 2004 (17 adult females, 10 adult males, 13 juveniles). Some individual red squirrels were mapped in multiple years (5 in all 3 years, 10 in 2 years, and 58 were mapped only once). Of the 53 focal middens, some were mapped in multiple years (13 in all 3 years, 14 in 2 years). Only 4 individuals (3 females and 1 male) changed their primary midden during the study. Mean territory size was smallest in 2002 (0.280 ± 0.028 ha), and was significantly larger in 2003 (0.411 ± 0.027 ha) and 2004 (0.401 ± 0.033 ha; (ANOVA on ln-transformed territory size, $F_{2,90} = 4.85$, $P = 0.010$); there was no significant difference in mean territory sizes in 2003 and 2004 (*t*-test, $t = 70$, $P = 0.394$).

Mean cone production per tree varied annually. Based on cone counts of 170 trees systematically located around the study area, in 2002, the mean number of cones per tree was 105 ± 14, 23 ± 4 in 2003, and 34 ± 5 in 2004. Similar to territory sizes, 2002

was significantly different than 2003 and 2004 (ANOVA, $F_{2,169} = 16.45$, $P < 0.0001$). Within a year cone production varied spatially (Figure 6-1). The spatial variation in cone production was high each year, with coefficients of variation of 2.20 in 2002, 2.78 in 2003, and 3.10 in 2004. A small number of trees produced the majority of cones. Of the 458 trees present across all 4 years of cone production data (2002-2005), 42 trees or 9.4% of the sampled trees, produced 50% of the cones. Looking at each year individually, in 2002, 4.8% of trees contributed 50% of the cones, and this was 3.3%, 3.7%, and 8.3% in 2003 to 2005, respectively. In addition, 84 trees (18%) did not produce cones in any year, while excluding the mast year of 2005 raises this to 157 trees (34%). Accounting for tree size (basal area) there was still considerable variation in cone production between individuals (Appendix 6). Kendall's coefficient of concordance, a descriptive measure of the agreement between multiple sets of rankings (Zar 1999), for cone production over all years by all sampled trees was statistically significant (Kendall = 0.522, $P < 0.0001$). Top-down concordance gives more weight to high ranks, and was 0.581 over all years, and 0.615 including 2002 to 2004 data only; indicating that some individual trees are consistently high cone producers.

TERRITORY SIZE & TERRITORY CONE LEVELS

Within years, the correlation (r_s) between territory size and the total number of cones contained within a territory was 0.687 in 2002, 0.493 in 2003, and 0.562 in 2004 (Figure 6-2). The r_s between territory size and territory cones over all years was much lower at 0.312; suggesting that over multiple years less than 10% of the variability in cone availability within a territory was explained by territory size. Among years, the

slopes of the relationship between territory size and the number of cones in a territory were significantly different (ANOVA, Territory size x Year interaction; $F_{2,87} = 5.99$, $P = 0.004$). The slope of the relationship in 2002 was steeper than both 2003 and 2004 (T-tests, 2002 vs. 2003: df = 2.97, $P = 0.005$; 2002 vs. 2004: df = 3.00, $P = 0.004$), but the latter two years did not differ significantly (2003 vs. 2004: df = 0.62, $P = 0.536$). Although the relationship between number of cones per territory and territory size varied among years, the total basal area of white spruce contained within territories was highly correlated with territory size over all years ($r_s = 0.846$).

The territory size of individual red squirrels was best explained by negative relationships with conspecific population density and the number of juveniles weaned by the owner during the year. Adult red squirrels had larger territories relative to juveniles (Tables 6-1 & 6-2). Females that successfully weaned offspring tended to have smaller territories than adult males and nonbreeding or failed breeder females (Appendix 7). This model, with an AIC_c weight of 0.391 and an R^2 of 0.366, was favoured 1.5 times more than the model that also included the mass of the owner. With the addition of mass, the R^2 value of this more complex model only increased by 0.01. The univariate model of age-class had an R^2 of 0.250, but a low AIC_c weight. The total number of cones available on a territory was best described by the age-class of the owner, with adults having more cones, and the local availability of cones within 0.1ha around the primary midden (Tables 6-3 & 6-4). This model explained 65.5% of the variation in territory cones and was favoured 1.7 times more than the second-best model that also included red squirrel population density. There was no significant difference between adult and juvenile red squirrels in the mean number of ln(cones) around their primary middens in either 2003 or

2004 (T-tests; 2003: df = 30, $P = 0.658$; 2004: df = 38, $P = 0.168$; only 1 juvenile was sampled in 2002). Adding population density to the favoured model increased the R^2 slightly (by 0.004). Weaning juveniles did not influence the quantity of cones in a territory (Appendix 7); being dropped early in the backwards-stepwise elimination modelling procedure. Cone density alone, although not favoured based on AIC_c weights (0.002), had an R^2 of 0.604.

Twenty-seven of the 93 territory owners mapped during the study (29%) did not survive overwinter. Mortality tended to be higher among individuals with fewer cones and smaller territories (Figure 6-3). The model including only territory size was favoured over twice as much as the model including both territory size and territory cones for predicting overwinter survival (Tables 6-5 & 6-6). This model successfully predicted 17 of 27 instances of mortality, and 41 of 66 instances of overwinter survival. This discrimination was considered acceptable with a ROC score of 0.702. Surviving individuals tended to have larger territories (Tables 6-7) with a predicted cut-off for survival of 0.33 ha based on the logistic regression. This result is consistent with a comparison of the mean territory size of individuals that survived and died overwinter; individuals that survived had a larger mean territory size than individuals that did not survive (Table 6-5). Individuals surviving overwinter tended to have more cones in their territory on average, but this was not statistically significant (Table 6-5). Of the individuals owning small territories (< 0.33ha), nine of 12 individuals with greater than 7600 cones survived overwinter (Figure 6-3). Juvenile territory owners had higher overwinter mortality than adults, with 58% of juveniles and 22% of adults not surviving.

Reproductive success

Reproductive success of the adult females that survived overwinter was quantified in three ways: i) producing a litter, ii) having at least one offspring successfully emerge from the nest, and iii) having at least one offspring successfully wean. Of the 39 adult females that survived overwinter, 31 (79%) produced a litter. The females that reproduced had more cones in their territory, although not significantly (Table 6-7). ROC scores for discrimination between the successful and unsuccessful groups were low for both and territory size and territory cone models (Table 6-6). Although cone production in fall 2003 was the lowest of the three years, 93% of females that survived overwinter had a litter. Of the surviving females, 14 (36%) had at least one juvenile emerge from the nest. These females had significantly more cones than females that did not successfully have any juveniles emerge and there was no significant influence of territory size (Tables 6-5 & 6-7). The logistic regression model for successful emergence of juveniles based on territory cones alone was favoured almost three times more than the model including both territory cones and territory size, and 21 times more than the model with territory size alone (Table 6-6). The discrimination between these groups based on the model with territory cones was acceptable with a ROC score of 0.720. Seventeen of the 25 females that did not have juveniles emerge, and 9 of 14 that did were successfully predicted. No females from 2003 had any juveniles emerge from the nest the following spring. Based on the logistic regression, the minimum number of cones on a territory for predicted juvenile emergence was approximately 9200. Females that weaned offspring were best described by the number of cones in her territory rather than territory size (Table 6-6). The mean number of cones was

significantly greater in territories of females that successfully weaned offspring (Table 6-5), but this was not significant in the logistic regression (Table 6-7). The ROC score for separating females that did and did not successfully wean offspring based on territory cones alone was 0.662.

DISCUSSION

Although red squirrels maintain individual food-based territories (C. Smith 1968), there was considerable variation in both the size and number of cones in individual red squirrel territories within white spruce habitat. Red squirrel territory size and territory cone levels were positively correlated within years; however, over all years the correlation was low. Territory size was not an equivalent measure of white spruce cone resources contained within a territory across years, nor was territory size adjusted such that all individuals had equal access to cones. This lack of a relationship between territory size of individual red squirrels and their territory cone levels was because cone production by white spruce was both spatially and temporally variable. Conifer seed appears very important for red squirrel reproductive success, although in low cone years, larger territories may contain alternate food items that may enhance overwinter survival of individuals, when available. For example, based on the results here a 0.4 ha territory could have virtually no cones, or up to 20,000 cones, depending on the year and the local cone conditions. Therefore, caution be used when equating territory size to food abundance, or assuming that resources are homogenously distributed when a population lives in single habitat type.

DETERMINANTS OF TERRITORY SIZE & CONE LEVELS

Adult red squirrels had significantly larger territories with more cones than juveniles. Besides age-class, territory size was negatively influenced by both population density and the number of juveniles weaned during the year. Age-class and the local cone density surrounding the primary midden influenced the total number of cones in a territory. Other individual and local habitat attributes contributed little additional information to the variation in territory size and territory cone abundance. That adults had larger, more cone rich territories may have been due to adults having established territories, whereas juveniles would own smaller territories, having only recently established theirs. Juveniles may establish in the system by getting part of the maternal territory, or by setting up a small territory between other territories. Kemp and Keith (1970) suggested that juveniles might survive in suboptimal areas until prime territory sites become vacant. Only four individuals moved their territory during the study, and none of these were juveniles. Juveniles tended to have relatively small territories containing few cones and may be why juveniles had lower overwinter survival than adults. However, some juveniles (6 of 13) with small territories containing few cones (<3200) survived overwinter. By spring all these surviving juveniles had increased their territory to include additional middens compared to their pre-caching fall territories.

The number of juveniles weaned negatively affected territory size. Female red squirrels have been reported to sometimes give a portion or all of their territory to their offspring; potentially increasing the offspring's chance of overwinter survival (Price & Boutin 1993; Berteaux & Boutin 2000). Of the 16 females that successfully weaned offspring during the summer before fall territories were mapped at least one offspring

settled on part of the natal territories of half the females, and one female bequeathed her entire territory to one of her offspring. Only 3 females that successfully weaned offspring did not survive overwinter, and none of their offspring had settled on their territories. Although territories tended to be smaller with an increase in the number of offspring weaned there was no effect of the number of offspring weaned on the total number of cones contained within territories; this may partly explain why female red squirrels perform this 'territory giving' behaviour.

Red squirrel population density declined from 2002 to 2003 and was then fairly constant in 2004. Mean territory size was the smallest in 2002, increased in 2003, and was then approximately the same size in 2004. This was similar to the relationship of mean territory size and population density found in other species with contiguous territories (Adams 2001; Steury & Murray 2003). If regional mean annual cone production determined territory size, 2003 would have had the largest territory size, then 2004 and 2002. This was not the case. Local cone conditions surrounding the primary midden had no significant effect on territory size, but had a significant effect on the cone resources available within territories. Tree size and microsite conditions affect cone production (Greene & Johnson 1994; Greene et *al.* 2002), resulting in some individual trees being consistently good cone producers. This has also been observed in other species. A minority of ponderosa pine (*Pinus ponderosa*) and oak (*Quercus* spp.) trees have been shown to produce the majority of cones and acorns, respectively, with individual production rankings of trees being significantly concordant year to year (Linhart & Mitton 1985; Greenberg 2000). This suggests spatial variation in the

production of plant seed is likely across many species, and could have implication for the amount of seed available in seed predator territories.

The results here do not agree with the prediction of Rusch & Reeder (1978) that red squirrel territory sizes are constant and set to provide adequate food resources during low cone years. Over all years, 29% of the red squirrels monitored here did not survive overwinter. Mean territory size was not constant across all years, and both territory sizes and territory cone levels were highly variable among individual red squirrels within a year. Historically, red squirrels in this system had much smaller mean annual territory sizes that tended to fluctuate with population density (Chapter 4). It is easier for individuals to increase territory sizes when population density is low rather than when it is high (McNair 1987). Red squirrel densities from 2002-2004 were the lowest observed in the study (1986-present; Boutin data); low population density could permit the large territory sizes observed. However, they were still not large enough to contain adequate food resources for all individuals. Disturbance caused by the removal of cone producing trees by spruce beetles could also affect territory size by reducing resource density directly and consequently population density. There was no significant negative relationship between live white spruce basal area and territory size; in fact the relationship was positive. Based on the literature it was unlikely that maximum defendable territory sizes had been reached. In mixed conifer forests, Steury & Murray (2003) found red squirrels had mean territory sizes of 0.76 ha, at the upper end of the range of territory sizes in this study. In Alberta, Rusch & Reeder (1978) reported territory sizes of 0.24 ha and 0.66 ha in white spruce and jack pine forests, respectively.

ENERGETIC REQUIREMENTS, AVAILABLE RESOURCES & ALTERNATIVE FOODS

Individual overwinter survival and reproductive success varied among individuals depending on their territory size or territory cone levels, rejecting the prediction that all individuals would have equal access to resources and equal performance. Territory size, and not the number of cones in a territory, was a better predictor of overwinter survival during this study. This result was unexpected because conifer seed is a dominant food source of red squirrels. However, this does not suggest that a supply of spruce cones are unimportant, but that when cone availability is low, alternative foods may be critical for overwinter survival of red squirrels.

A recent study determined mean winter field metabolic rates (FMR) of red squirrels of 196 kJ · day^{-1} (Humphries et *al.* 2005). Extrapolated over 7 months, from mid-October when caching is complete and remaining white spruce cones open to release their seed, until mid-May when snow melt occurs, an individual would require 41160 kJ of energy. White spruce seeds contain 0.0293 kJ · mg^{-1} (dry weight; M. Smith 1968), with an average seed mass of 2.0 mg (Greene & Johnson 1994) and an average of 48 sound seeds per cone (Beaulieu et *al.* 1998). To survive overwinter solely on spruce seed, an individual would require a cache of approximately 14600 cones, or 70 cones a day. This threshold is well above the cones contained in three-quarters of the territories, but this high a level of overwinter mortality was not observed. Brink & Dean (1966) estimated that red squirrels likely consumed 40 to 50 cones per day in winter based on cache sizes in Alaska, therefore the remaining energy must come from supplemental foods.

Red squirrels are efficient cone harvesters, removing up to 100% of the cones from individual trees (Peters et *al.* 2003). However, the years of study here were relatively low cone years, with the previous cone mast occurring in 1998 (Chapter 5). Squirrels also consume conifer buds and cache mushrooms and consume them overwinter and in early spring (M. Smith 1968; Rusch & Reeder 1978; Steele 1998; Currah et *al.* 2000). Conifer buds provide less energy than seeds at 0.0209 kJ · mg^{-1} (dry weight) and can comprise up to 50% of a squirrel's diet when cones are low, but it is unlikely red squirrels could survive on buds alone (Smith 1967). At 50% of the diet, the number of cones required to survive overwinter was reduced to 7300; this seems more consistent with the 7600 cones in small territories of individuals that survived overwinter.

Mushrooms may comprise part of the diet when cones are extremely low, and when available, containing 0.0191 kJ · mg^{-1} (dry weight; Smith 1967). Since mushrooms are 85-90% water (Smith 1967) and do not contain much mass even when dry, a large volume of mushrooms would have to be consumed to obtain comparable energy to seed. Larger territories may contain more mushrooms, as their availability is both spatially and temporally variable (LaMontagne & Boutin, unpublished data). Although cone availability was low in 2003, mushroom abundance was relatively high and many mushrooms were cached in 2003 compared to 2002 (Humphries et *al.*, unpublished data). The availability of mushrooms in 2003 when cones were low likely contributed to high overwinter survival of red squirrels, and supports the suggestion that buds and mushrooms are important supplemental food for red squirrels (M. Smith 1968). In years and (or) locations of both low cone and low mushroom availability I would expect that

overwinter mortality would be much higher. I did not test this expectation because data were not available on the spatial distribution of mushrooms.

The minimum number of cones required for successfully producing a litter, based on logistic regression, was 7200. This was similar to the resources required for overwinter survival based on red squirrel energetics and 50% of the diet being spruce seed. However, in the spring following the low cone year (2003), 12 of the 13 adult females that survived overwinter reproduced, but none of these females had juveniles emerge from their nest. Similar to other studies (Larsen & Boutin 1994; Humphries & Boutin 2000) most adult female red squirrels produced a litter, regardless of the resources available. Reproducing even under poor conditions might be an adaptation to living in a highly variable environment if the cost of producing a litter is energetically low. However, 9200 cones was the cut-off based on logistic regression for juvenile emergence from the nest, suggesting that a supply of seed was critical for reproductive success. Red squirrels are income breeders, relying on resources recently consumed during the reproductive period (Drent & Daan 1980), and the nutrition contained in white spruce seed is important to body condition (Brink & Dean 1966). Lactation is energetically expensive (Humphries & Boutin 2000) and having seed resources available may be important at this stage of reproduction. Cones available in the current year could influence juvenile weaning, since after emergence juveniles have been observed feeding on their own (LaMontagne, personal observation).

Errors in classifying observed overwinter survival and reproductively successful adult females (after birth) based on the fit of the logistic regression models could be due to time lags in cone production, predation, having a small but good quality territory, or

taking over additional middens due to mortality of neighbours. Time lags could play a role in overwinter survival because cones are cached. If this study had taken place immediately following or one year after a mast year, cached resources could affect an individual's ability to survive overwinter (M. Smith 1968; Gurnell 1984). Lags were not considered here because mean cone production in the area was low since the 1998 mast year. However, local lags in cone production could also explain how individuals with small territories with few cones survived overwinter. Winter weather conditions may also cause variation in overwinter energy requirements, but no differences were detected in the mean monthly minimum temperatures here.

Because this study took place in a natural environment, predation could affect all individuals, regardless of the food available in their territory. Steury & Murray (2003) found an inverse relationship between territory size and mortality, suggesting individuals with smaller territories had fewer resources and therefore spent more time searching for food, or were nutritionally limited, increasing their vulnerability to predation. Individuals with large territories but few cones could also suffer increased predation due to increased search times for food. Very few predation events were detected during the study (7 confirmed mortalities included 3 predation events and 4 due to unknown causes, perhaps starvation, during the overwinter period). A relationship between predation risk and cone availability in a territory could not be determined. When rearing offspring, having few cones may require females to spend more time foraging, with an increased predation risk. Based on territory size, 25 individuals were not predicted to survive overwinter but did. Some of these territories may have contained sufficient cones to allow survival due to the spatial variation in cone production. For example, 9 individuals with territories smaller

than 0.33 ha but contained more than 7600 cones survived overwinter. Also, six individuals owning small fall territories containing fewer than 3200 cones also survived (all juveniles), but by spring they increased their territory to include additional middens than they did during pre-caching territory mapping. Within the area gained there could have been cones or mushrooms cached by the previous owner that aided survival.

There was large range of both territory sizes and resource levels, and the benefits of a small territory or one with few cones must have the potential to outweigh the costs of not having a territory at all. Some species occupying year-round territories rarely change their territory locations once established (for example: red squirrels: C. Smith 1968; Price et *al.* 1986; Boutin et *al.* 1993; Larsen & Boutin 1995; Berteaux & Boutin 2000; Ural owl (*Strix uralensis*) pairs: Lundberg 1981; and numerous tropical passerines: Rowan 1966; Morton 1980). Territory owners may continue to defend their territory even during times of low food resources, perhaps because they risk moving into an area with even lower food production, their territory contains other resources like nest sites, or defending the territory now protects it for later times when resources are higher. Although the costs of territorial defence were not explicitly considered here, the range in territory size and the number of cones in territories could occur because there may be considerable variation between the minimum number of resources required for survival and the point where the maximum benefit is achieved (Kodric-Brown & Brown 1978). In addition, familiarity with a territory and its neighbours may allow higher survivorship, increased foraging efficiency, and a reduction in the energy needed for territorial defence (Larsen & Boutin 1995). This settlement pattern is unlike many avian species that move into an area and settle territories in order from good to poor (Newton 1998).

Here, territory size and the available cones per territory were quantified, but not the resources actually cached by individuals. Individual differences in caching behaviour and total cache sizes could provide further insight into how individuals compensate for locations and periods of low availability of the primary food item. Many studies have used surrogates for territory quality based on food, for example, habitat composition and (or) distance to preferred habitat (Ferrer & Donázare 1996; Hazlitt 2001; Breininger & Carter 2003; Kerbiriou et *al.* 2006). In addition, even after food supplementation, considerable variation in individual performance is detected, presumably because territories differed in their initial quality (Svensson & Nilsson 1995). Based on the results here, spatial and temporal variation of resources affects food resource levels within territories and individual performance *within* a single habitat. Further areas of research include quantifying individual variation in territory food levels during a resource pulse, relating male reproductive success to territory cone levels, and investigating caching behaviour. Implications for the spatial variation in food availability include individual fitness and may also include increasing population persistence during times of low mean food availability (Łomnicki 1988).

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Table 6-1: Stepwise and main-effects models of factors influencing ln(red squirrel territory size (m^2)) with the number of parameters (n_i), ΔAIC_c, AIC_c weights (w_i) and R^2. Age-classes are 'adults' or 'juveniles', mass is the lowest mass recorded in August (g), density is conspecific density, BA density is the basal area of spruce >5cm dbh in a 0.1ha buffer of the primary midden, cone density is ln(total cones in the 0.1ha buffer).

Model – Territory size	n_i	ΔAIC_c	w_i	R^2
age-class + num. juvs weaned + density	5	0.000	0.391	0.366
age-class + num. juvs weaned + density + mass	6	0.824	0.259	0.376
age-class + num. juvs weaned + density + mass + cone density	7	1.397	0.195	0.388
age-class + num. juvs weaned + density + mass + cone density + age-class*mass	8	3.359	0.073	0.391
age-class + num. juvs weaned	4	4.138	0.048	0.321
age-class + num. juvs weaned + density + mass + cone density + age-class*mass + cone density*mass	9	5.677	0.023	0.392
age-class + num. juvs weaned + density + mass + cone density + BA density + age-class*mass + cone density*mass	10	8.176	0.007	0.392
age-class + num. juvs weaned + density + mass + cone density + BA density + age-class*mass + density*mass + cone density*mass	11	10.742	0.002	0.392
age-class	3	11.200	0.001	0.250
age-class + sex + num. juvs weaned + density + mass + cone density + BA density + age-class*mass + density*mass + cone density*mass	12	13.375	<0.001	0.392
mass	3	32.006	<0.001	0.062
num. juvs weaned	3	35.776	<0.001	0.023
constant only	2	35.841	<0.001	0.000
density	3	35.988	<0.001	0.021
cone density	3	37.419	<0.001	0.006
BA density	3	37.760	<0.001	0.002
sex	3	37.922	<0.001	0.001

Table 6-2: Parameter estimates for the best red squirrel territory size model (ln(red squirrel territory size (m^2)). Standard errors are robust errors adjusting for repeated sampling of focal middens.

parameter	coefficient	standard error	*t*	*P*
age-class	0.730	0.100	7.33	<0.001
(juv = 0, adult = 1)				
num. juvs weaned	-0.160	0.076	-2.11	0.040
density	-0.234	0.095	-2.47	0.017
constant	8.031	0.192	41.73	<0.001

Table 6-3: Stepwise and main-effects models of factors influencing the total number of white spruce cones in a territory, quantified as ln(total number of cones in territory). See Table 6-1 for explanation of table contents.

Model – Total territory cones	n_i	ΔAIC_c	w_i	R^2
age-class + cone density	4	0.000	0.513	0.655
age-class + density + cone density	5	1.106	0.295	0.659
age-class + density + mass + cone density	6	3.238	0.102	0.660
age-class + density + mass + cone density + age-class*mass	7	4.611	0.051	0.664
age-class + density + mass + cone density + age-class*mass + cone density*mass	8	6.068	0.025	0.667
age-class + density + mass + cone density + age-class*mass + density*mass + cone density*mass	9	8.118	0.009	0.668
age-class + sex + density + mass + cone density + age-class*mass + density*mass + cone density*mass	10	10.337	0.003	0.669
cone density	3	10.701	0.002	0.604
age-class + sex + num. juvs weaned + density + mass + cone density + age-class*mass + density*mass + cone density*mass	11	12.907	0.001	0.669
age-class + sex + num. juvs weaned + density + mass + cone density + BA density + age-class*mass + density*mass + cone density*mass	12	15.543	<0.001	0.669
age-class	3	83.509	<0.001	0.134
density	3	90.919	<0.001	0.062
mass	3	92.307	<0.001	0.048
constant only	2	94.706	<0.001	0.000
num. juvs weaned	3	95.838	<0.001	0.011
BA density	3	95.919	<0.001	0.010
sex	3	96.009	<0.001	0.009

Table 6-4: Parameter estimates for the best model of the cones contained in red squirrel territories (ln(total number of cones within territory)). Standard errors are robust errors adjusting for repeated sampling of focal middens.

parameter	coefficient	standard error	*t*	*P*
age-class (juv = 0, adult = 1)	0.765	0.242	3.16	0.003
cone density	0.697	0.072	9.74	<0.001
constant	2.906	0.578	5.03	<0.001

Table 6-5: Mean (± SE) attributes of fall territory size and territory cones for individuals that survived overwinter, and of the adult females surviving overwinter, the same attributes for females producing a litter, having one or more juveniles emerge from the nest, and having one or more juveniles successfully wean. T-tests were conducted for overwinter survival, with a two-sided test for territory size, and a one-sided test for cones in the territory; and one-sided tests for reproductive performance. One-sided tests were used for female performance, to test if females that performed better had access to more cones on average than individuals that performed poorly.

Term	Did not survive overwinter (n = 27)	Survived overwinter (n = 66)	*t*	*P*
ln(cones in territory)	8.149 (0.235)	8.536 (0.171)	-1.261	0.105
ln(territory size in m^2)	7.872 (0.097)	8.219 (0.057)	-3.209	0.002
	No litter produced in spring (n = 8)	Females produced litter in spring (n = 31)		
ln(cones in territory)	8.215 (0.609)	8.924 (0.181)	-1.892	0.068
ln(territory size in m^2)	8.271 (0.161)	8.359 (0.070)	-2.127	0.293
	No juvs emerged (n = 25)	Juvs. successfully emerged (n = 14)		
ln(cones in territory)	8.440 (0.245)	9.384 (0.237)	-2.528	0.008
ln(territory size in m^2)	8.324 (0.080)	8.371 (0.112)	-0.347	0.365
	No juvs weaned (n = 29)	Juvs. successfully weaned (n = 10)		
ln(cones in territory)	8.583 (0.228)	9.384 (0.295)	-1.795	0.040
ln(territory size in m^2)	8.320 (0.081)	8.403 (0.091)	-0.559	0.290

Table 6-6: Logistic regression results of models for the influence of territory size (ha) and territory cone quality (estimated total number of cones in territory) on overwinter survival and adult female spring reproductive success (producing a litter, having juveniles reach emergence).

Model	ΔAIC_c	w_i	ROC
Overwinter Survival			
territory size	0.000	0.658	0.702
territory size + territory cones	1.526	0.308	0.715
territory cones	5.932	0.034	0.616
Adult females producing a litter in spring			
territory cones	0.000	0.474	0.601
territory size	0.449	0.378	0.581
territory size + territory cones	2.327	0.148	0.585
Adult females with successful offspring emergence			
territory cones	0.000	0.708	0.720
territory size + territory cones	1.987	0.262	0.731
territory size	6.360	0.029	0.547
Adult females with successful offspring weaning			
territory cones	0.000	0.663	0.662
territory size + territory cones	2.215	0.219	0.659
territory size	3.461	0.177	0.547

Table 6-7: Logisitic regression parameters and odds-ratios with 95% confidence intervals for the best models based on AIC_c weights influencing red squirrel overwinter survival and adult female spring reproductive success (producing a litter, having juveniles reach emergence). Models include either territory size (ha) or territory cone quality (estimated total number of cones in territory in 10000's).

Model	*b*	OR	*z*	*P*
Overwinter Survival				
territory size	4.354	77.752	2.61	0.009
	(1.085, 7.622)	(2.960, 2042.282)		
Adult females producing a litter				
territory cones	0.338	1.402	0.73	0.466
	(-0.569, 1.244)	(0.566, 3.472)		
Adult females with offspring emerging				
territory cones	0.901	2.463	2.18	0.029
	(0.092, 1.711)	(1.097, 5.532)		
Adult females with offspring weaning				
territory cones	0.621	1.860	1.75	0.080
	(-0.073, 1.315)	(0.929, 3.724)		

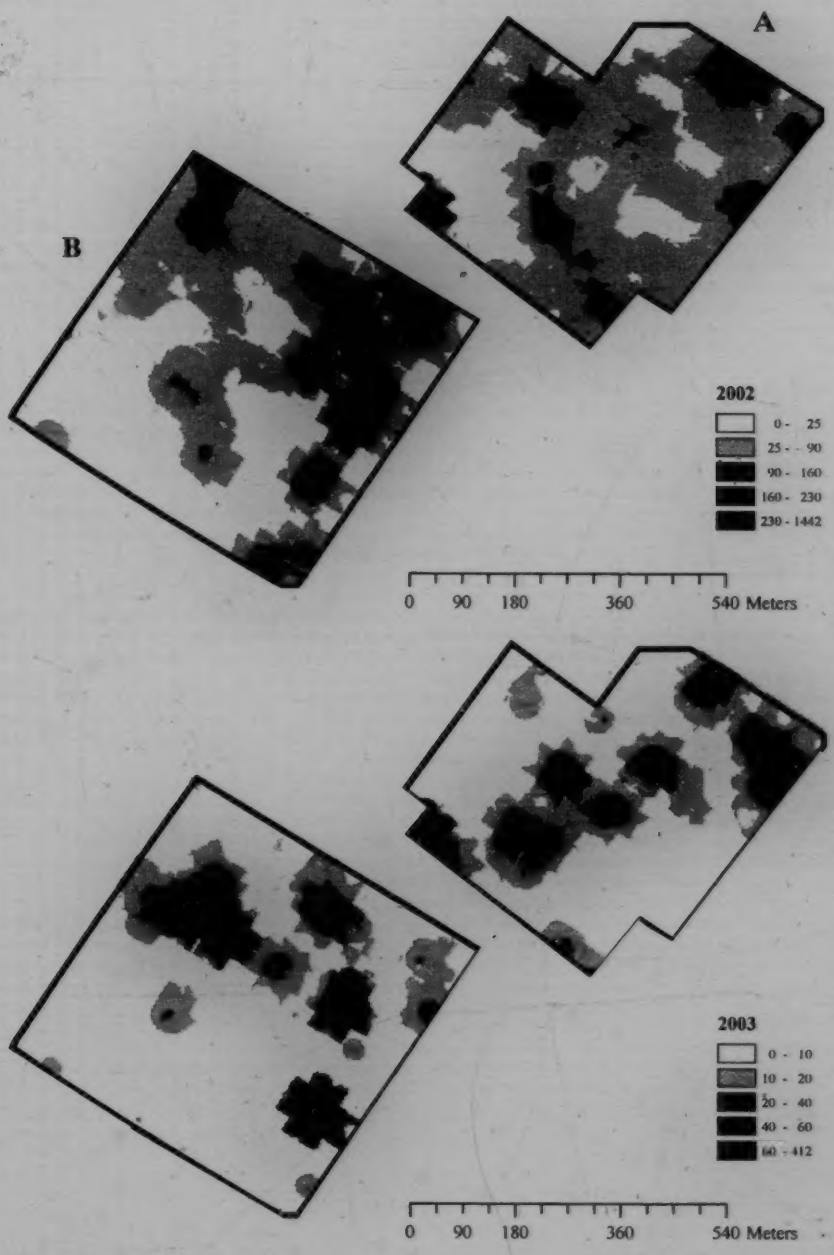

Figure 6-1. See next page for caption.

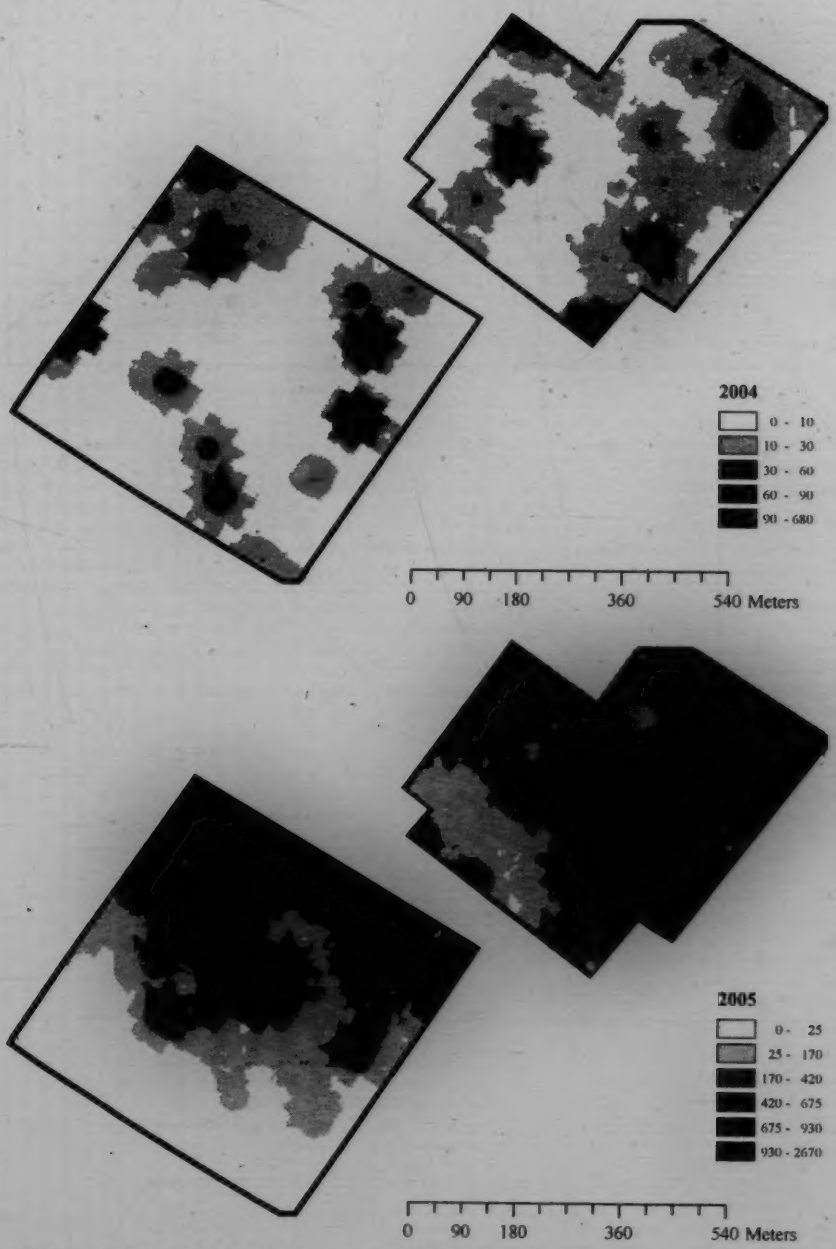

Figure 6-1: Spatial and temporal variation in pre-caching white spruce cone density (cones · $10m^{-2}$) in 2002 to 2005. Plot A is at the top, B at the bottom (indicated in first panel). Note that legend scales differ among years. White shows low, and darker greys and black showing the areas of higher cone production in each year.

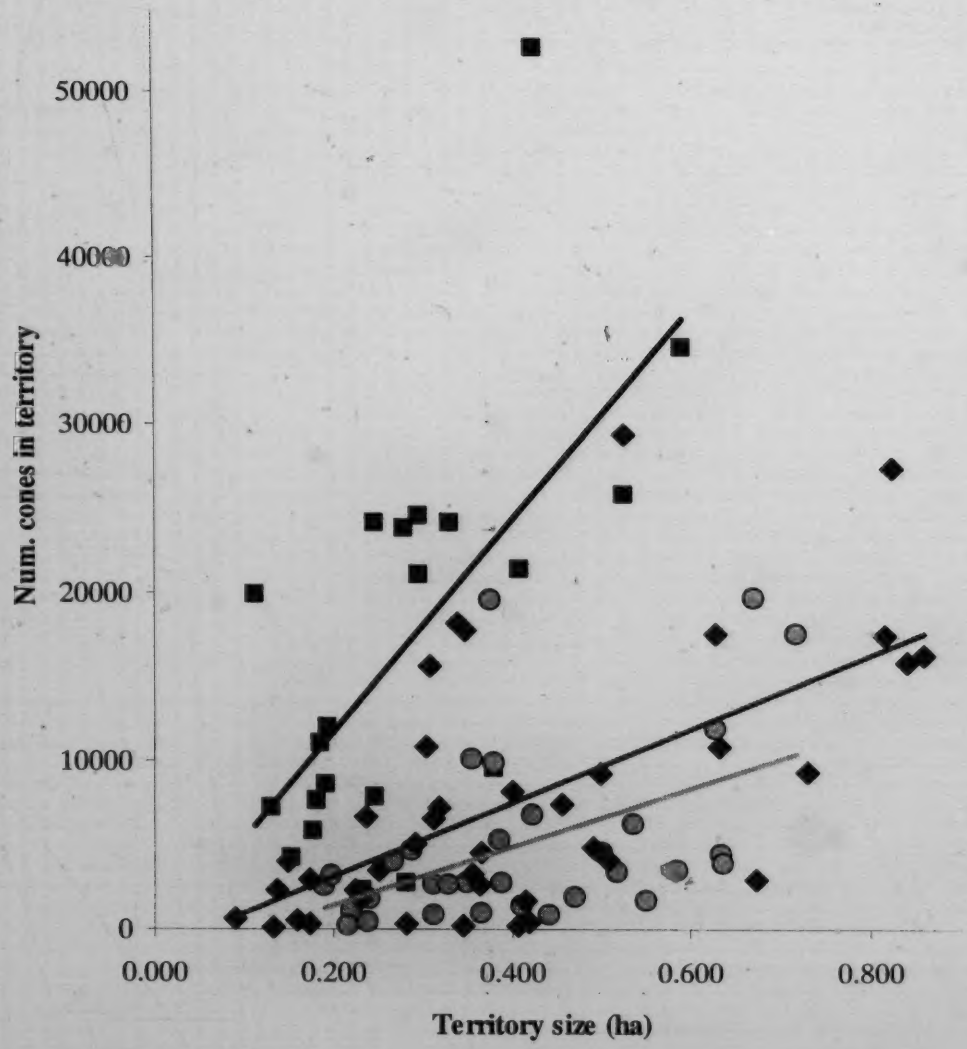

Figure 6-2: Territory sizes and the total number of white spruce cones contained within individual red squirrel territories mapped in late-July to mid-August, 2002 to 2004. Lines show the linear relationship in each year. Annual data are shown as filled squares (2002, n = 21), light grey circles (2003, n = 32), and dark grey diamonds (2004, n = 40).

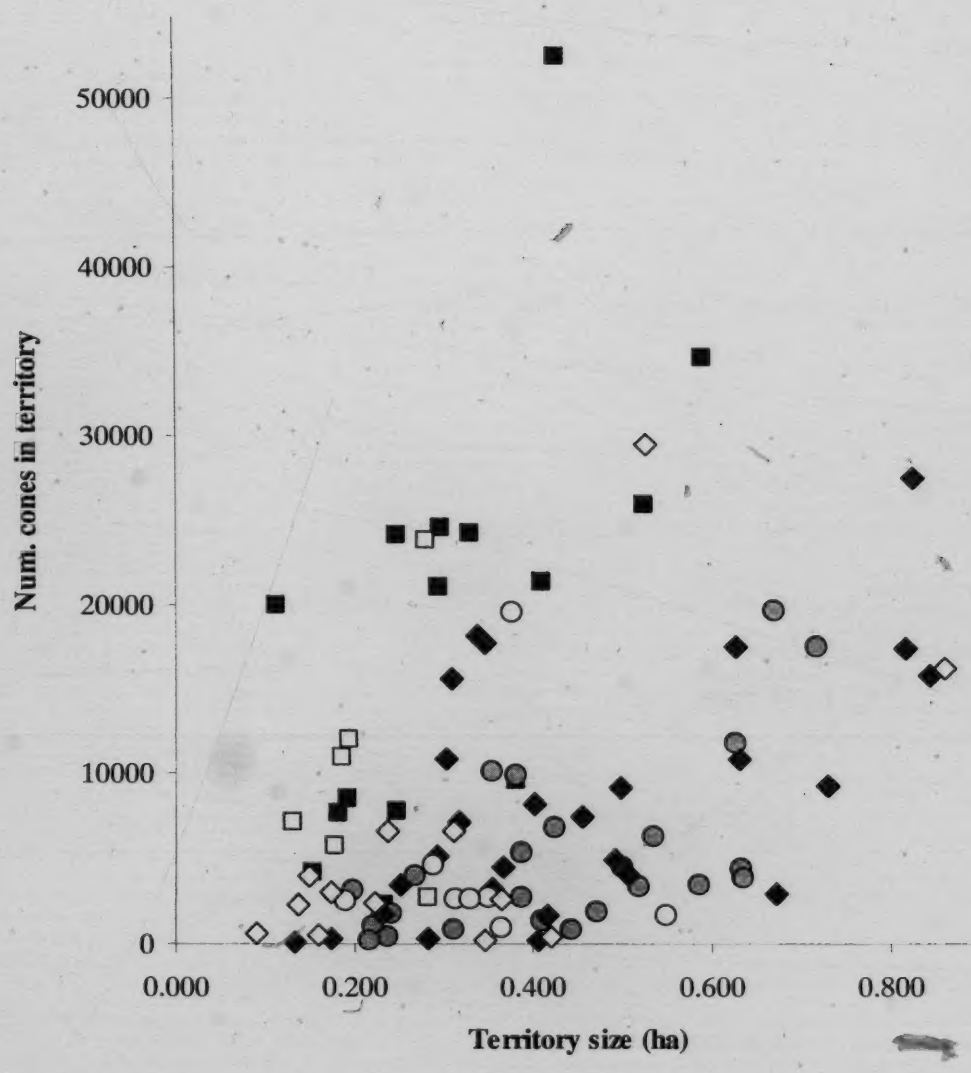

Figure 6-3: Relationship between territory size and the total number of white spruce cones contained within the territory and whether individuals survived (shaded symbols, colours are the same as in Figure 6-2) or did not survive (open symbols) overwinter, measured as surviving until the May midden census (n = 93). Data for all years is shown as squares (2002), circles (2003), and diamonds (2004).

CHAPTER 7

VARIATION IN INTRASPECIFIC FOOD AVAILABILITY IN RED SQUIRRELS: EFFECTS ON SURVIVAL, REPRODUCTION, & SHORT-TERM POPULATION PERSISTENCE

INTRODUCTION

Individual variability is the basis of the most general ecological theory, natural selection (Łomnicki 1988). However, when state variables are used to describe a population (i.e., total population size or population density), variation among individuals is ignored. For example, population density is used to infer per-capita food availability to individuals in the population. A change in per-capita food availability through increased intraspecific competition (i.e., density) is thought to be a mechanism by which density dependence can occur. The idea is that as population density increases, per-capita food declines, and with it the population growth rate ($r = \ln(N_{t+1}/N_t)$) via reduced reproductive rates, or increased mortality rates of individuals (Begon et *al.* 1996). It has been suggested that with a large temporal variation in food abundance, a more relevant measure of the effect of density on intraspecific competition for food is the number of individuals per amount of food, and not the conventional measure of the number of individuals per area (Newton 1998). Both approaches assume that average per-capita food is an adequate representation of the resources available to all individuals in a population (Stenseth 1980; Uchmański 1999). By definition, these measures will reflect average values and by themselves, do not capture variation among individuals created by such factors as spatial variation or intraspecific variation. Inferring per-capita resources based on density alone, as opposed to incorporating the variability that exists, likely has repercussions on expected

performance of individuals within the population (e.g., survival, reproductive success) relative to their energetic requirements.

It is typically very difficult to estimate the resources available to individuals in natural systems (Łomnicki 1988; Boutin 1990). The inability to quantify resources has limited our ability to examine the distribution of food resources among individuals within a population compared to the assumption of equal per-capita food, and its consequences. Individual performance (survival, reproduction) is linked to food abundance, and has often been shown in food supplementation experiments (Boutin 1990; Adams 2001). It has been hypothesized that variability in individual performance can have implications at the population level, including increased population persistence and reduced fluctuations in density (Łomnicki 1988; Uchmański 1999). For example, if there is substantial positive skew in the distribution of food among individuals the likelihood of some individuals having adequate food availability for survival, and thus expected short-term population persistence, should increase. This is because even under low food conditions some individuals should have adequate resources even if the majority of individuals do not. In comparison, in times of low food, per-capita food may fall below energetic requirements for survival, altering predictions.

Studying a species that maintains individual, non-overlapping territories may allow the distribution of food per individual to be examined relative to assuming equal per-capita food. For North American red squirrels (*Tamiasciurus hudsonicus*) food (primary conifer seed) is an important determinant of population dynamics (Kemp & Keith 1970; Chapter 4). Also, territory size and the quantity of cones within an individual's territory vary, and influences overwinter survival and reproductive success

(Chapter 6). Here, I examined the distribution of white spruce (*Picea glauca*) cones across all individual territories in a population of red squirrels. Then I contrasted the observed distribution of cones with an assumption of equal distribution for meeting energetic requirements, and I predicted the proportion of individuals that would survive overwinter. I analysed each year separately because resources can be temporally variable and the consequences of these food availability assumptions (equal per-capita or distribution of food) may differ depending on the annual food conditions. Other individual attributes that could affect survival and reproductive success were not considered here (e.g., age, mass, natal environment, maternal effects, genetics; Caswell 2001; LaMontagne & McCauley 2001; Ferrer & Bisson 2003; Nilsen et *al.* 2004; Kerbiriou et *al.* 2006; Reid et *al.* 2006).

METHODS

I studied variation in white spruce cone availability in individual red squirrel territories and expectations for individual performance in a 36 ha and a 26.5 ha study plots in the south-western Yukon, Canada (61°N, 138°W) from 2002 to 2005. White spruce was the dominant vegetation in the area and the only conifer species. White spruce has years of complete cone failure, when virtually all trees produce zero cones, years of low-intermediate cone production, and mast years (Dale et *al.* 2001; Chapter 5). Red squirrels occupy individual non-overlapping territories year-round (Gurnell 1984). Food is cached in a central midden (Smith 1968; Smith 1981) and red squirrels are active throughout the winter (Pruitt & Lucier 1958). In the boreal forest, red squirrels rely heavily on conifer seeds and a territory with a central cache of cones (a midden) is considered essential for

overwinter survival (C. Smith 1968; Steele 1998). Complete annual red squirrel population censuses were conducted in May and August. See Humphries & Boutin (2000) and Chapters 4 & 6 for more information on trapping.

VARIATION IN CONE AVAILABILITY

I created annual spatial maps of cone production within the study area by multiplying the annual distribution of live white spruce basal area and the cone production per unit basal area using the raster calculator in ArcGIS 9.0. (See Chapter 6 for further details).

CONES AVAILABLE TO INDIVIDUALS

Unequally distributed cones

I estimated the distribution of the number of cones available to each territory owner in each population prior to cone caching. For each year, I calculated the number of cones per territory with a model including the age-class of the owner (adult or juvenile) and the local cone density within a 0.1ha area surrounding the primary midden. The equation was: $\ln(\text{territory cones}) = 2.906 + 0.765 \cdot \text{age-class} + 0.697 \cdot \ln(\text{local cone density})$. Age-class was known from trapping records (Boutin data), with zeros representing yearlings and one for adults (Chapter 6). I obtained the cone density in a 0.1ha area surrounding the primary midden from each annual cone density layers using Zonal Statistics in Hawth's Tools (Beyer 2004; Chapter 6). Other variables such as sex, mass, number of juveniles weaned, and population density did not help to explain additional variation in

the territory cone levels (Chapter 6), therefore I did not include them in estimates of the number of cones available in individual territories.

I transformed the ln-cone estimates to total cones per territory and adjusted for logarithmic transformation bias (Sprugel 1983) by multiplying by the correction factor of 1.371. The correction factor was based on the residuals of the predicted back-transformed values compared to the raw observed values following a log-log regression on a set of territories where the cone abundance was known (from Chapter 6). I assumed that the number of cones in the territory represented the cones available for individuals to cache, and would affect overwinter survival and future reproductive success. I also assumed the relationship between age-class and local midden cones to total cones available within a territory were the same for all years.

Equally distributed cones

For each population and each year I calculated the per-capita cones available by dividing the total amount of cones available in red squirrel territories, from above, by the number of squirrels in the August census. I examined how the total number of cones encompassed by red squirrel territories was divided among individuals. For each year and each population I tested the goodness of fit of the distribution of cone availability in individual territories to the normal, uniform, exponential, and gamma distributions; the expected distributions were generated with parameters estimated from the territory data (Sokal & Rohlf 1995). I used Shapiro-Wilk tests for investigating deviations from the normal distribution, and Kolmogorov-Smirnov tests for the other distributions. I also tested the distribution of cones among territories for significant skew, occurring when the

skewness statistic is more than two times the standard error of skew (SES); a normal distribution would produce a skewness statistic of approximately zero (Tabachnick & Fidell 1996).

EXPECTED PERFORMANCE

I examined the consequences of predicting overwinter survival and successful reproduction of individuals from average per-capita food compared to the distribution of cones per individual territories. I used 7300 cones as the number required for individual overwinter survival from energetic requirements of red squirrels (Humphries et *al.* 2005; Chapter 6). I assumed that white spruce seed comprised at least 50% of the energy obtained. Up to 50% of the winter diet of red squirrels can be conifer buds, but they cannot survive on a diet of buds alone (Smith 1968). Similarly, individuals with small territories, where it was unlikely that alternative food dominated the diet, showed a similar threshold of 7600 cones for overwinter survival (Chapter 6). In the case of equal resource availability among individuals, if the mean number of cones in the territories exceeded the threshold for individual survival, 7300 cones, all individuals would be expected to survive. On the other hand, if the mean number of cones contained in territories were less than the threshold, no individuals would be expected to survive.

For adult females (1^+ years old in the August census), based on previous logistic regression analysis (Chapter 6), a threshold of 9200 cones was used to determine if females would be successful breeders the following spring based on at least one juvenile emerging from the nest. Similarly, if the per-capita cones for adult females were less than 9200 cones, none would be predicted to successfully reproduce in spring. For the

distribution of cones in individual territories, I recorded the proportion of individual territories that had more cones than the threshold for individual survival and adult female reproduction. I then examined the similarities and differences in the performance of individuals and population-level predictions based on per-capita cones and the distribution of cones among individuals.

RESULTS

DISTRIBUTION OF CONE RESOURCES AMONG INDIVIDUALS

Cone production varied spatially and temporally (Figure 7-1), and the estimated number of cones in individual territories varied considerably (Figure 7-2; Appendix 8). While the mean number of cones per territory in each plot varied from about 5,500 to 67,000 cones annually, the number of cones available to individuals over all years ranged from 24 to over 200,000 cones (Table 7-1). The number of cones per territory was the lowest in 2003 (for both means and at the upper end of the range) and 2004. There was no significant difference in the mean-ranked sum of cones per territory in these years (Kruskal-Wallis: Population A, $\chi^2 = 0.646$, $P = 0.422$; Population B, $\chi^2 = 1.071$, $P = 0.301$). The mean-ranked sum of cones per territory differed significantly for all other combinations of years for both populations.

The distribution of cones in individual territories differed significantly from a normal distribution in all years for both populations (all $P < 0.03$; Table 7-2). The distributions of cones per territory were all truncated at values above zero (Figure 7-2), and in population A there was a significantly positive skew in all years; this was similar for population B, with the exception of 2005 when there was no significant skew (Table

7-2). There tended to be more individuals with fewer cones, and few individuals with many cones available in their territory (Figure 7-2). The distributions of cones in territories were better fit by either exponential or gamma distributions with a long tail showing the skew in the distribution of cones among individual territories (Appendix 9). The annual distribution of territory cone data consistently differed from a uniform distribution. For both populations, in the years with higher cones (2002 and 2005) the distribution was most similar to the gamma distribution (all $P > 0.40$). A prominent hump showed that few individuals had very poor quality territories, many individuals had a moderate level of cones relative to other individuals, and there was a long tail of more cone rich territories. In the years with lower cone availability, many red squirrel individuals had few cones and few individuals had many cones; in these years the distribution was closest to the exponential distribution (all $P > 0.18$) or the gamma distribution (B-2003, $P > 0.66$; Appendix 9).

PREDICTIONS OF OVERWINTER SURVIVAL & REPRODUCTIVE SUCCESS

Using per-capita cones, and a 7300-cone threshold for overwinter survival of red squirrels, 100% of individuals in both populations were expected to survive overwinter in 2002, 2004, and 2005. Neither population was predicted to have any individuals survive in 2003 (Table 7-1), but this did not occur because the actual red squirrel population was present in 2004. Conversely, based on the distribution of cones in individual territories, in all years at least some individuals had sufficient cones for overwinter survival, but usually not all individuals (Figure 7-2). The exception was population A in 2005, where all individuals had more than 7300 cones on their territory. If the entire winter diet of red

squirrels was white spruce seed, 14,600 cones would have been required. In this case, based on per-capita food no individuals would be expected to survive overwinter following in the low cones years of 2003 and 2004. In all years, population A would be expected to have some individuals survive based on a distribution of cones, regardless of if cones comprised 50% or even 100% of the red squirrel diet.

For female reproductive success, with equal per-capita cones all females in both populations were expected to have at least one juvenile reach emergence in the years following 2002 and 2005 (Table 7-1). In 2003, since no individuals had adequate per-capita cones for overwinter survival, it follows that no females would have had enough cones for reproduction. Although all individuals were expected to survive overwinter in 2004 based on per-capita cones, there were still not sufficient cones for females to be reproductively successful. Assuming variation in the cones available to individuals, similar to the results for overwinter survival, in each year at least some females were expected to be reproductively successful, ranging from 22% to 100% annually.

Comparing the observed overwinter survival of individuals in the red squirrel field populations to the predictions here, there were differences in the predicted number of individuals to survive overwinter based on the distribution of cones per individual, and those that actually did survive. For example, in 2002, more individuals were predicted to have sufficient cones to survive overwinter than actually did. For population B, individuals in 61 of 70 territories (87%) had ≥7300 cones in 2002, while 52 squirrels (74%) were present in the May 2003 census (Boutin, unpublished data). On the other hand, 2003 was the lowest cone year and only 15 of 54 individuals (28%) had the

predicted number of cones sufficient for overwinter survival, but 41 individuals (76%) actually survived. These trends were similar for population A.

DISCUSSION

The average amount of food per individual has been suggested to better represent per-capita food resources than a measure of population density alone, especially when there is high temporal variability in food (Newton 1998; Lindström et *al.* 2005). However, here I detected considerable variation, and significant skew in the food available to individuals in a population. Differential food availability will have consequences on individual performance and population persistence. Assuming equal food availability lead to incorrect predictions about 1) individuals surviving overwinter in a very low food year, and 2) whether females would have reproductive success in another relatively low cone year. On the other hand, because of the significantly skewed distribution of food among individuals (in most years), some individuals were always expected to survive overwinter. In all years at least some females were expected to have offspring emerge from the nest. One year was an exception; following the cone mast of 2005 numerous cones were available throughout the study area. After this year nearly all individuals were expected to survive, and females to be reproductively successful, regardless of how the resources were considered (per-capita vs. the unequal distribution among individuals).

Since the local cone production surrounding a midden is a significant determinant of the territory cone availability (Chapter 6), the temporal and spatial availability of cones likely has considerable influence on the availability of cones among individuals. In the very low food years (2003, 2004) cone availability was low over most of the area

occupied by the population and relatively few individuals had territories in areas of good cone production. Cone availability in territories during these very low food years was reflected in the tendency for a negative exponential distribution of territory cones levels. In relatively higher food years (2002, 2005) fewer areas had low cones, much of the area had comparably higher cones and there were even some cone-rich areas. This resulted in a gamma-distribution of resources in these years. It is not surprising that these distributions fit the patterns of food availability. These are good candidates to fit skewed data and furthermore the shape of these distributions are related (Rice 1988). The shape of the gamma distribution depends on two parameters, a shape parameter and a scale parameter, and, if the shape parameter is equal to one, the gamma distribution coincides with the exponential distribution (Rice 1988).

This chapter reports on the use of average per-capita food availability on expectations for survival and reproductive success using a threshold approach. There are important caveats to be noted here. The threshold for survival was calculated from field metabolic rate measurements of red squirrels and was extrapolated over the entire winter, and I assumed it was the same for all individuals. I also assumed the seed from white spruce cones was the critical resource and that 50% of the diet must be from cones for an individual to survive. There is some variability among individuals in their field metabolic rate (Humphries et *al.* 2005), but this variability is likely relatively minor compared to the range of cones contained within red squirrel territories, so the overall results should remain consistent regardless of the inability here to pinpoint an exact threshold. Furthermore, territory size varies (Chapter 6) and larger territories may contain alternative food that may be available for overwinter consumption (Smith 1968),

or individuals may acquire adjacent middens if neighbours die. Red squirrels can also cache mushrooms, and consume them overwinter (Smith 1968). Based on white spruce cones alone, the general result of the highly skewed distribution of the availability of food among individuals holds. But, not including mushrooms is certainly a source of error when comparing the results to the actual population. Individual overwinter survival can also be affected by the predation independent of territory cone availability.

Regarding the measures of per-capita food availability and subsequent predictions, I did not include variation around the mean. This was because given a pool of resources and a number of individuals the mean is an intuitive calculation, but the level of variability around the mean is much less so. This is one of the criticisms of using density to infer per-capita resources, that individual variability is ignored (Łomnicki 1988). If the availability of cones followed a normal distribution, the result here that the skewed distribution is important for some individuals to survive overwinter in poor cone years, would change little if the standard deviation, and hence the variation around the mean, was considered to be small. Regardless, the results here showed that the distribution of food among individuals was not normally distributed.

Some individuals occupied territories with relatively low cone availability, and were thus predicted to not survive overwinter. It is unknown why individuals might choose to settle in poor areas. Red squirrels in this area rarely change territories (Chapter 6) perhaps because the potential cost exceeded the potential benefit (Price et *al.* 1986; Larsen & Boutin 1995). Alternative food resources, if available, could enable overwinter survival of individuals in territories of North American red squirrels with poor cones, or individuals could wait and acquire additional middens if neighbours die overwinter

(Chapter 6). Furthermore, in a spatially variable area, if individuals move they may incur the risk of ending up in a lower quality area, increased predation risk etc.

There was a large amount of variability in the range of cones available in individual territories. Spatial heterogeneity in the local availability of cones and individual attributes determined the number of cones available to an individual. Adults had more cones in their territories than juveniles; consequently many of the territories with lower cone availability belonged to juveniles, and led to lower overwinter survival of this age-class. Low juvenile survival tends to be observed in the wild (Larsen & Boutin 1994; Chapter 6).

Assumptions that individuals live in homogeneous habitats and that population density alone are an adequate representation of the per-capita resources for all individuals within the population is often used. This approach has been successful in describing some general population patterns (Grimm 1999; Hastings 2005). With temporally variable food resources, using per capita food based on both food and density may be more informative about the roles of density and food on population dynamics (Newton 1998; Lindström et *al.* 2005). However, when per-capita food was compared to the expected energetic requirements of individuals, allowing food availability to vary among individuals provided a better approximation for the expectations of overwinter survival than assuming identical individuals. For example, the mean number of cones per individual in 2003 was 5582 in population A. However, with a skewed distribution of food availability among individuals some individuals were expected to survive, not because this mean food level is what individuals require to survive, but because some individuals had sufficient resources for survival while others did not. Furthermore,

following 2003 and 2004, no adult females would be expected to have juveniles emerge from the nest based on per-capita cones, whereas between 25 – 58 % of the adult females would have sufficient resources based on the distribution of cones in individual territories.

The influence of individual variability on population dynamics and the increased understanding that can be generated by examining individuals are some of the main arguments for the individual-based approach (Grimm et *al.* 1999; DeAngelis & Mooij 2005). The spatial distribution of resources and individual consumers can affect future population size (Hancock et *al.* 2005). Łomnicki (1980) developed a model that incorporated spatial heterogeneity and individual differences that arose from unequal resource partitioning based on a social hierarchy. His model suggested that within a population, individuals with the highest ranks would typically have sufficient resources for maintenance and perhaps reproduction, while individuals lower in the hierarchy would have access to fewer resources that may not meet maintenance costs. Here, individual variability was assessed only as a function of the availability of the primary food item in territories and its effects on overwinter survival and female reproductive success, and I did not extend this to population fluctuations. There are other sources of individual variation that affect individual performance and potentially population dynamics that I also did not consider. These include maternal effects (LaMontagne & McCauley 2001; McAdam & Boutin 2003), age or size class distribution (Caswell 2001).

Here, the distribution of the primary food resource within a territorial social structure was examined. In a similar sense, Wauters et *al.* (2001) found that the proportion of high quality habitat in individual home ranges was positively correlated

with breeding success of female Eurasian red squirrels (*Sciurus vulgaris*). In a non-territorial species, the home range of female roe deer (*Capreolus capreolus*) vary in quality and can affect the birth date of fawns, their weight in early fall, and the quality of the home range occupied by fawns the following winter (Nilsen et *al.* 2004). It has also been shown empirically that spatial heterogeneity in vegetation can affect the influence of population density on a large mobile forager due to selective feeding (Wang et *al.* 2006). The results here support the predictions from simulation studies incorporating individual variation in that individual performance can affect the dynamics of populations, at least with respect to persistence and the magnitude of density variation. Further research can look at the effects of individual variation under field conditions on population fluctuations, and individual-based simulation models could be constructed for this system. The spatial and temporal variation in territory food levels and thus individual performance could affect population dynamics compared to average food and average individuals, as shown here for population persistence.

The insight gained from information on resources available to individuals may help in understanding how individuals contribute to population-level dynamics, above that of grouping individuals into simply age-classes or individuals residing in poor versus good quality habitat-types. In the latter case, only some element of chance would determine individual performance, without the biological link to food resources. Not only the annual mean per-capita food availability, but also the distribution of food among individual consumers, will influence the performance of individuals and can have implications at the population-level. A given population size may represent different distributions of individual attributes that can have effects at the population scale (Grimm

et *al.* 1999; Hancock et *al.* 2005). Nature is heterogeneous, if heterogeneity occurs at a scale that creates differences among individuals, population density or per-capita resource levels will not adequately represent individuals in the population. Further studies investigating the distribution of resources among individuals, how these patterns develop, and the consequences of this variability may help us to understand mechanisms behind population change beyond stating the importance of population density or food.

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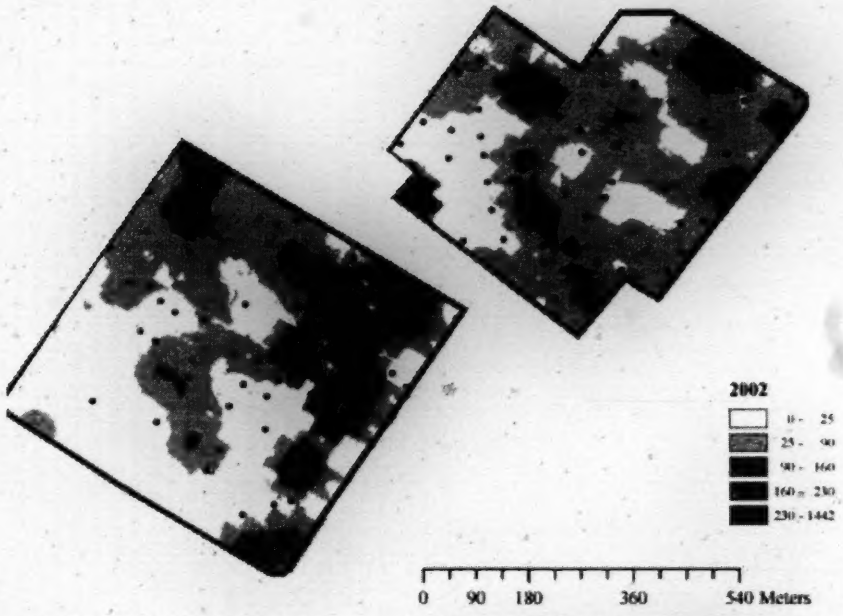
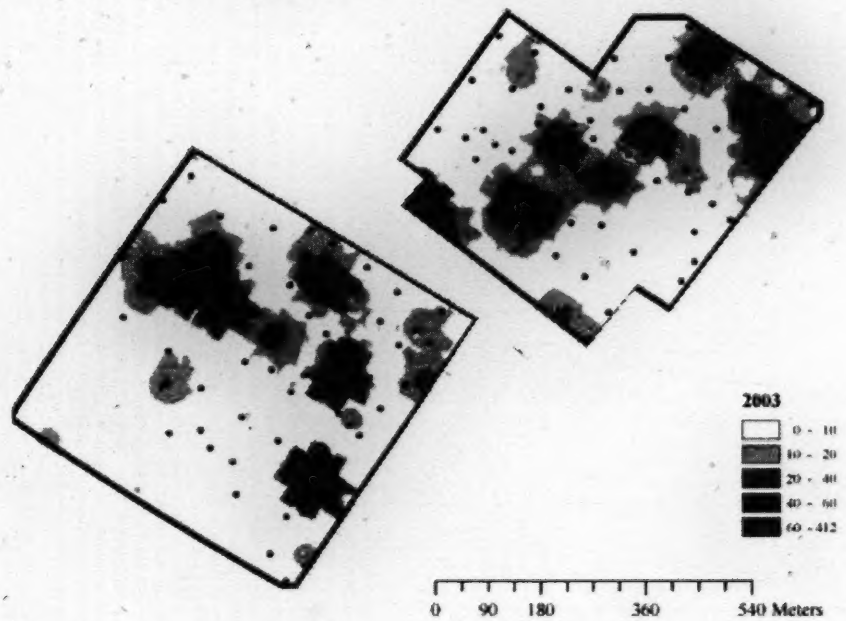
Table 7-1: Summary of the mean (per-capita) cones per individual and the range of cones per individual red squirrel territory, and the proportion of individuals exceeding thresholds for overwinter survival and female reproductive success. The thresholds for overwinter survival (7300 cones), and for adult female reproduction the following spring (9200 cones for juvenile emergence from the nest based on adult females only (ratio of successful females / total females shown)). 'N' is the population size each year. Bold shows when the proportion based on per-capita cones is zero.

			Equal partitioning		Unequal partitioning	
			Per-capita cones		Distribution of cones	
Year	N	Mean territory cones (range)	Survival ≥7300	Reproduction ≥9200 (Females only)	Survival ≥7300	Reproduction ≥9200 (Females only)
Plot A						
2002	77	20631 (454 – 76303)	1.00	1.00	0.90	0.87 (20/23)
2003	**58**	**5582 (172 – 15048)**	**0.00**	**0.00**	**0.31**	**0.25 (4/16)**
2004	43	8165 (24 – 33894)	1.00	**0.00**	0.37	**0.58 (7/12)**
2005	66	67347 (8656 – 205527)	1.00	1.00	1.00	1.00 (13/13)
Plot B						
2002	70	24141 (3477 –93550)	1.00	1.00	0.87	0.86 (19/22)
2003	**54**	**6202 (54 – 33684)**	**0.00**	**0.00**	**0.28**	**0.22 (4/18)**
2004	43	7743 (97 – 25819)	1.00	**0.00**	0.44	**0.43 (9/21)**
2005	65	57083 (916 – 180365)	1.00	1.00	0.91	0.89 (25/28)

Table 7-2: Summary statistics for normality and skewness tests of the distribution of white spruce cones among individual red squirrels in the southwest Yukon, in each of 2002 to 2005. When the skewness statistic is greater than 2 times the standard error of skew (SES) there is significant skew present.

		Normality			Skew		
Year	N	W	Z	*P*	Skewness statistic	2 x SES	Significant skew?
Plot A							
2002	77	0.857	4.919	<0.001	1.820	0.558	Positive
2003	58	0.923	3.034	0.001	0.762	0.643	Positive
2004	43	0.838	4.042	<0.001	1.264	0.747	Positive
2005	66	0.930	3.066	0.001	1.029	0.603	Positive
Plot B							
2002	70	0.887	4.217	<0.001	1.546	0.586	Positive
2003	54	0.753	5.383	<0.001	2.618	0.667	Positive
2004	43	0.893	3.167	<0.001	1.005	0.747	Positive
2005	65	0.958	1.940	0.026	0.546	0.608	no


2002
0 - 25
25 - 90
90 - 160
160 - 230
230 - 1442
0 90 180 360 540 Meters


2003
0 - 10
10 - 20
20 - 40
40 - 60
60 - 412
0 90 180 360 540 Meters

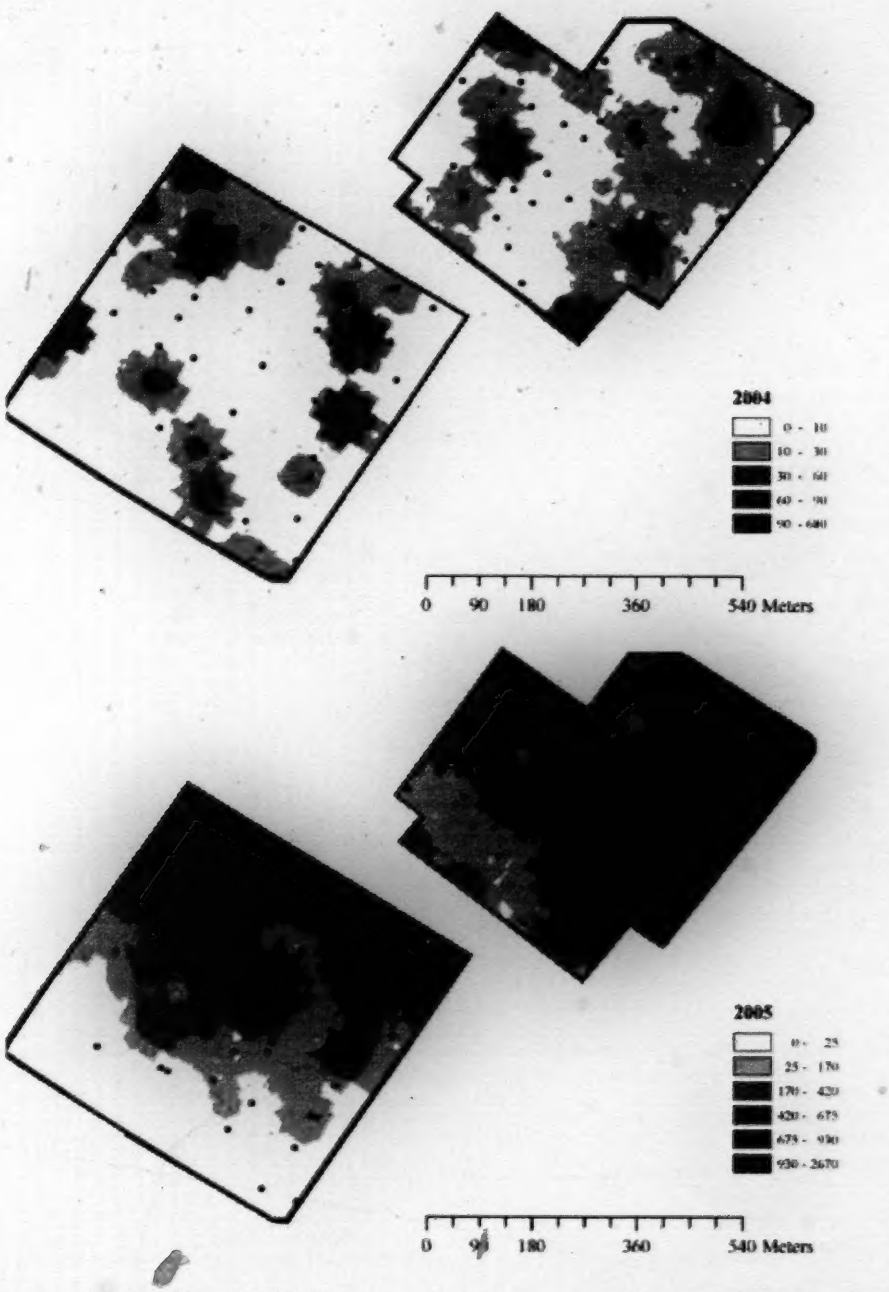


Figure 7-1: Spatial distribution of white spruce cone resources in each of 2002 to 2005. The legend represents the number of cones per $10m^2$ cells and the scale varies each year. The black circles show the location of all primary red squirrel middens within each study area each year. Population A is on the upper right and B is the lower panel.

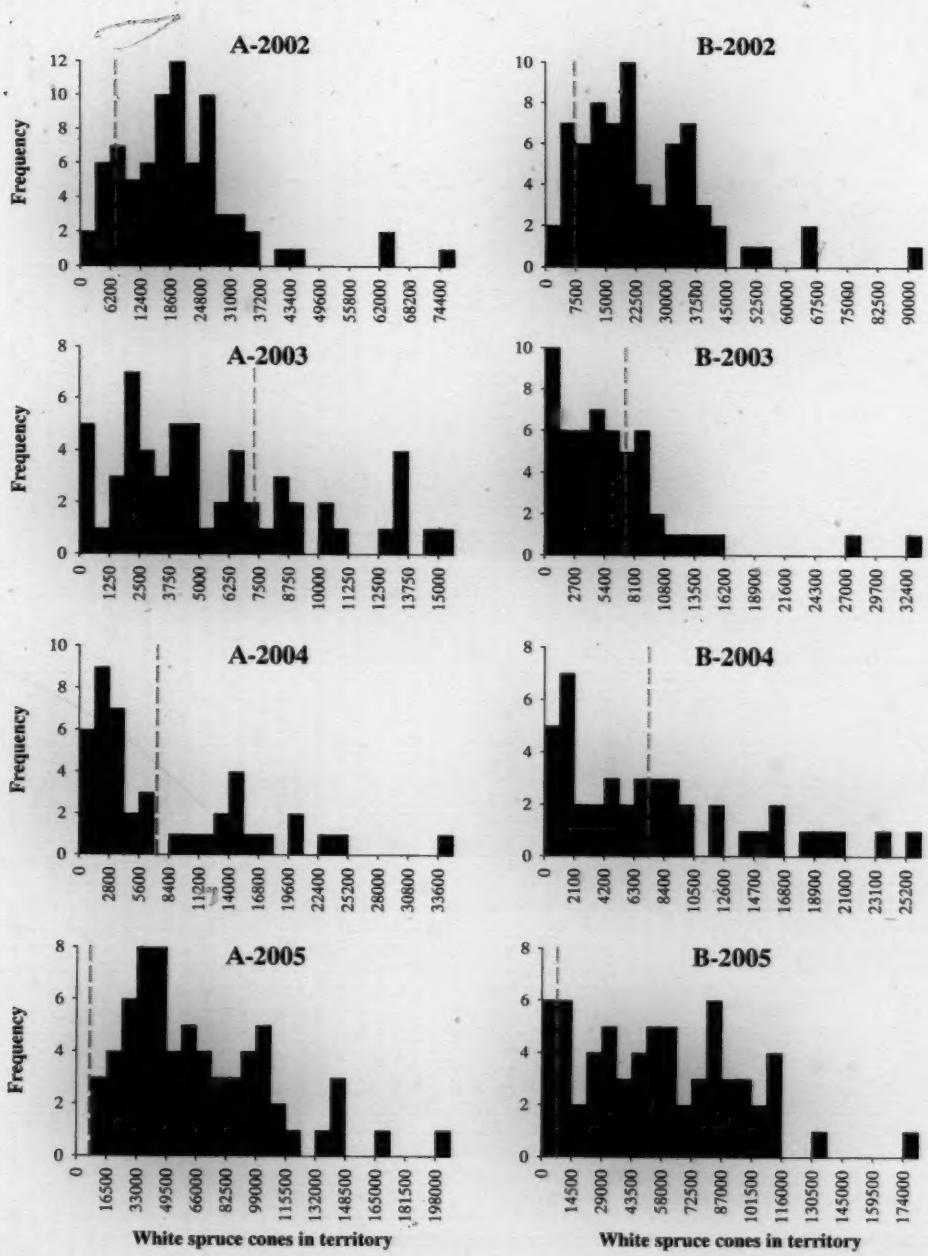


Figure 7-2: Frequency distribution of cones in individual red squirrel territories in two populations, A and B, from 2002 to 2005. Note that the x-axis and y-axis scales vary. The dashed line represents 7300 cones; based on energetics this is the minimum number of cones required for overwinter survival when cones comprise 50% of the diet.

CHAPTER 8

GENERAL DISCUSSION & CONCLUSIONS

Populations exist in variable environments. While much attention has been paid to temporal variation in resources and the response of populations or the average consumer, spatial variability in resources may result in differences in individual fitness; understanding the causes and consequences of this variation among individuals has become a current area of focus in ecology (Wiens 2000). Individual variation in performance is the basis of evolution by natural selection, and is therefore of interest above and beyond the average response of individuals (Łomnicki 1988). However, quantifying the primary resource available to individuals is typically difficult to achieve in nature (Łomnicki 1988; Boutin 1990). The objectives of this study were to:

1. quantify natural variation in food availability over time and space,
2. examine the relationship between territory size and territory food availability and the determinants thereof, and
3. investigate the consequences of variation in food resources to both population dynamics and individual performance.

To achieve these objectives I tested hypotheses regarding the effects of food abundance and population density on the population growth rate of red squirrels, I examined the spatial and temporal variation in the availability of the primary resource of red squirrels, white spruce cones through examining synchrony in the patterns of cone production of individual trees and created maps of cone production. I related spatial and temporal variation in food resources to individual performance, determined factors influencing

individual territory size, quality and subsequent surviving and breeding success, and I examined the potential effects of using per-capita food availability (total food / population density) versus the skewed distribution of food among individuals on the overwinter survival based on independently estimated energetic requirements. This study was only possible due to the detailed information available on resource levels, and was a unique attribute of this study. The results here showed that there was considerable variation in the availability of cone resources over both time and space and some of the potential impacts on individual performance.

SUMMARY OF RESULTS

In this study I used long-term data (1990-2005) on red squirrel population density and white spruce cone availability to show that red squirrel population growth was influenced more by food levels than by population density. More specifically, population growth from spring of time 't' to 't+1' was more strongly influenced by cones available in fall of year 't', presumably because of the related overwinter survival of juveniles, than by cones in 't-1' that would represent the energy resources available with which to produce juveniles. I also showed that there could be considerable variability in the synchrony in seed production among individual trees. This was the first study of its kind to examine a large data set of individual trees over a relatively small spatial extent, and may have implications for hypotheses of synchronous seed production by plant populations. There was variation in cone production patterns temporally, and large variation in the availability of cones spatially, likely due to individual tree and local site attributes (Greene & Johnson 2002).

The way resources are distributed among individuals within a population may influence the fitness of individuals and their relative contribution to the population growth (Łomnicki 1988). Using field-work (2002-2004), I showed that territory size was influenced by the age-class of the territory owner (adults had larger territories than juveniles), the number of offspring weaned (females successfully weaning more offspring had smaller territories), and population size negatively affected territory size. The age-class of the territory owner and the density of cones around the primary midden influenced the total number of cones contained within a territory. Population density and the number of juveniles weaned had no significant influence on the number of cones within a territory. Territory size and the number of cones within a territory tended to be positively correlated within a year, but there was no significant correlation over all years due to the high temporal variability in cone production. I suggest that caution be taken when assuming that territory size is equivalent to the resources available within a territory, especially over time when the resource is spatially and temporally variable.

The number of cones in a red squirrel's territory in fall was critical to females successfully having juveniles reach emergence from the nest the following year, whereas some individuals that had fewer cones within their territory still survived overwinter. Survival in a territory that had a small number of white spruce cones could occur because individuals with large territories may have had access to an alternative food, specifically mushrooms that can also be cached by red squirrels, or individuals with relatively small territories took over neighbouring middens left vacant after mortalities. Using the model developed here for the number of cones within an individual's territory, I estimated the cones available for every individual in the population in each of 4 years and calculated

the average per-capita cones. In the lowest seed year, using per-capita food incorrectly predicted that no individuals would survive overwinter. This agrees with predictions of Łomnicki (1988), Grimm (1999) and Uchmanski (1999) from a theoretical or simulation approach that individual variation can be important to population persistence.

In addition, two chapters (Chapters 2 and 3) show methods developed 1) to quantify cone production by individual white spruce trees based on a cone production index, and 2) to delineate mast years based on site-specific patterns for a variety of plant species. The white spruce cone production index should provide a better approximation of actual cone production than the conversion factors recently used in the literature but based on other tree species with a different growth form. The mast-year delineation chapter presents a potential method for standardising the way that mast-seeding years are discussed in the literature based on the description of mast seed years being periods of unusually large seed production (see Chapter 3). Currently, there is no standardised method consistently used, whether the focus was on the plants producing seed, or the effect of these mast-seeding events on consumer populations or community dynamics.

FUTURE RESEARCH

Density is commonly used to represent per-capita food, with the assumptions that food levels are constant and equally available to individuals and that increased population density subjects individuals to higher levels of intraspecific competition that leads to reduced performance by all individuals (Begon et *al.* 1996). However, if the availability of resources is skewed among individuals, this variability can have effects on not only the performance of individuals but at the population level as well (Grimm & Railsback

2005). Although it is often difficult to quantify variation among individuals, the food resources available to individuals, and components of individual fitness, studying systems where it is possible in nature should provide insight into why some individuals are more successful than others. There are a number of questions that could be followed up from my research, both from the perspective of individual variation in cone production that could contribute to our understanding of the phenomenon of mast seeding, to the causes and consequences of individual variation within consumer populations:

- What causes variation in cone production lags of individual trees (is it microhabitat, resource balance, genetics)?
- Is there a link between the spatial scale of high synchrony in cone production and the spatial scale of the dominant seed predator?
- Why do individuals not leave poor territories? What are the costs and benefits of remaining in a poor territory?
- How does spatial and temporal heterogeneity in resources affect lifetime fitness of individuals?
- Do individual lifetime fitness differences exist across the population? If so, are they related to midden location (local habitat quality)? How might this affect population dynamics (is there an intrapopulation source-sink dynamic)?
- Are juveniles that inhabit good quality territories good quality individuals (e.g., higher growth rate) or just lucky (e.g., mother bequeaths, proximity to dense resources)?
- Besides overwinter survival and breeding output, are there other advantages of living in a high quality territory (e.g., stress responses, male breeding success)?

- Cohort vs. local environment effects (are there cohort effects in red squirrels? Is there an interaction between local and annual resource availability that magnify or nullify cohort effects?)

Furthermore, I had initially intended on examining the productivity of red squirrels within populations, asking if the location of an individual would give a distinct fitness advantage, but the resurgence of a spruce beetle outbreak in 2002 made it difficult to identify if there were consistently good and poor cone producing areas. Spruce beetles do not infest trees randomly and instead typically select larger trees, with a front moving across the study area (LaMontagne, unpublished data). If, in undisturbed habitats, there was temporal consistency in the quality of individual territories across the population because microsite factors affect cone production (Greene & Johnson 2002), then we might expect this fitness advantage. There could also be a multi-generational effect, since juveniles typically settle relatively close to their mother's territory (Berteaux & Boutin 2000).

It is my hope that my dissertation will contribute to our knowledge of how variation in available resources contributes to differences in individual performance and that individual variation in both resource production and consequently individual performance could be important to population persistence. Although assumptions of identical individuals have been a long-standing tenant of ecological research, and classical population models have contributed much to the ways we view population fluctuations (Hastings 2005), understanding how individuals contribute to the observed dynamics will only help to further our understanding of ecological systems.

Territory size has been used a surrogate for the food available to an individual, when not assuming that individual territory size is adjusted in order to contain the same amount of food as all other individuals within the population. Without information on resource levels (such as food) within territories we have no direct way of evaluating the ecological significance of variation in territory size (Wiens et *al.* 1985).

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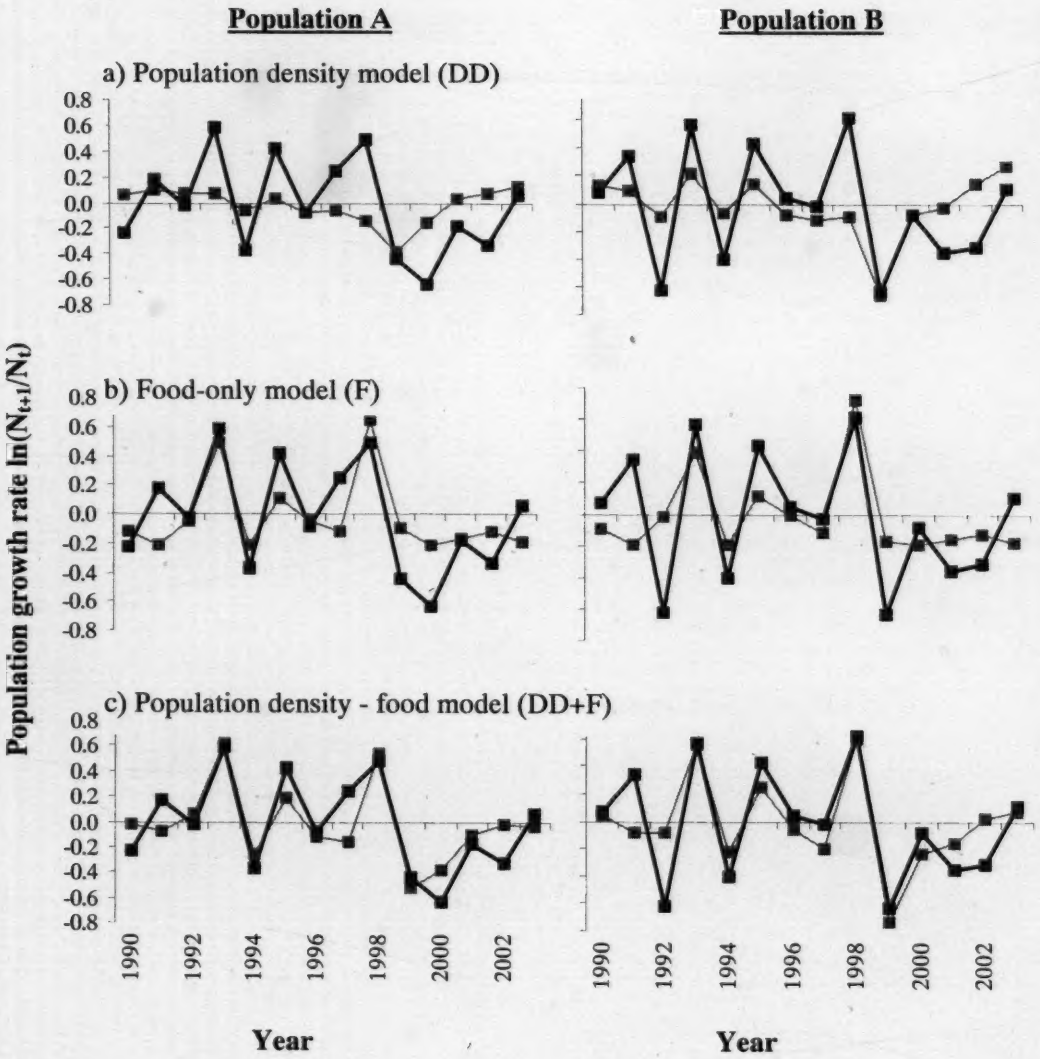
Appendix 1: The mean matrix for each population of red squirrels (A and B) based on transitions from 1990 to 2004 that was used for assessing sensitivity of lambda to variation in vital rates in life-table response experiments.

$$Mat_A = \begin{pmatrix} 0.141 & 0.553 & 0.365 & 0.356 \\ 0.614 & 0 & 0 & 0 \\ 0 & 0.684 & 0.280 & 0 \\ 0 & 0 & 0.242 & 0.434 \end{pmatrix}$$

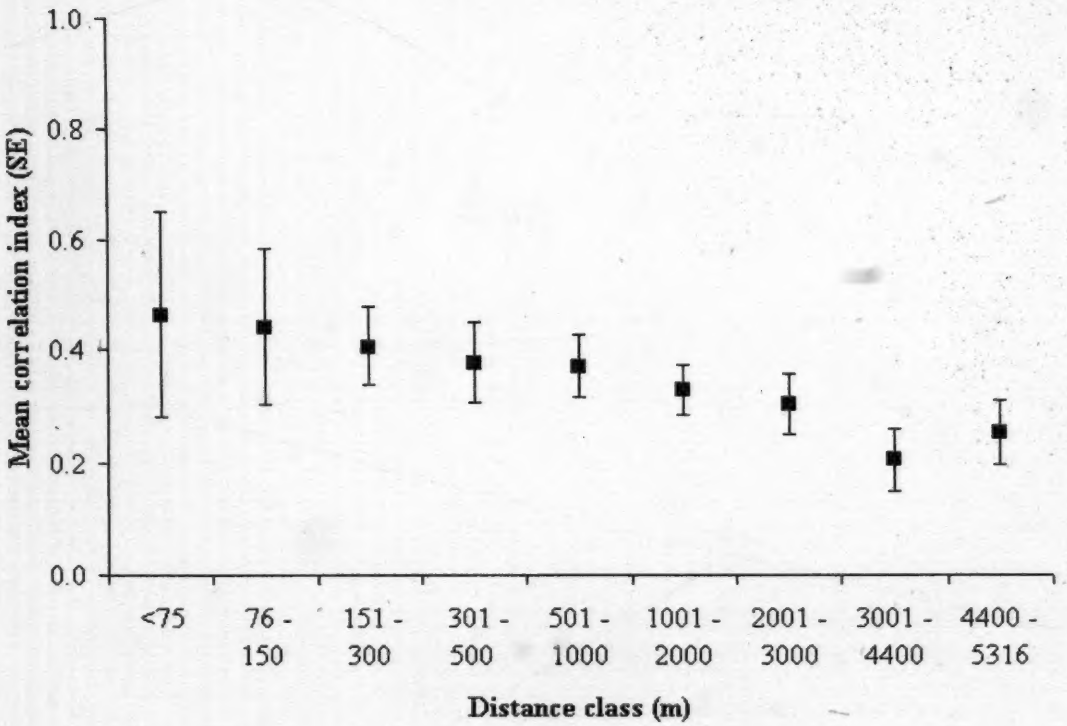
$$Mat_B = \begin{pmatrix} 0.180 & 0.300 & 0.450 & 0.246 \\ 0.716 & 0 & 0 & 0 \\ 0 & 0.671 & 0.376 & 0 \\ 0 & 0 & 0.261 & 0.309 \end{pmatrix}$$

Appendix 2: Lower-level vital rates of female red squirrels fertilities in age-classes: (1) 1-year olds, (2) 2-year olds, (3) 3-4 year olds, (4) 5+ year olds. '…' cells show no individuals in an age-class, or no juveniles present for basing lower-level vital rates.

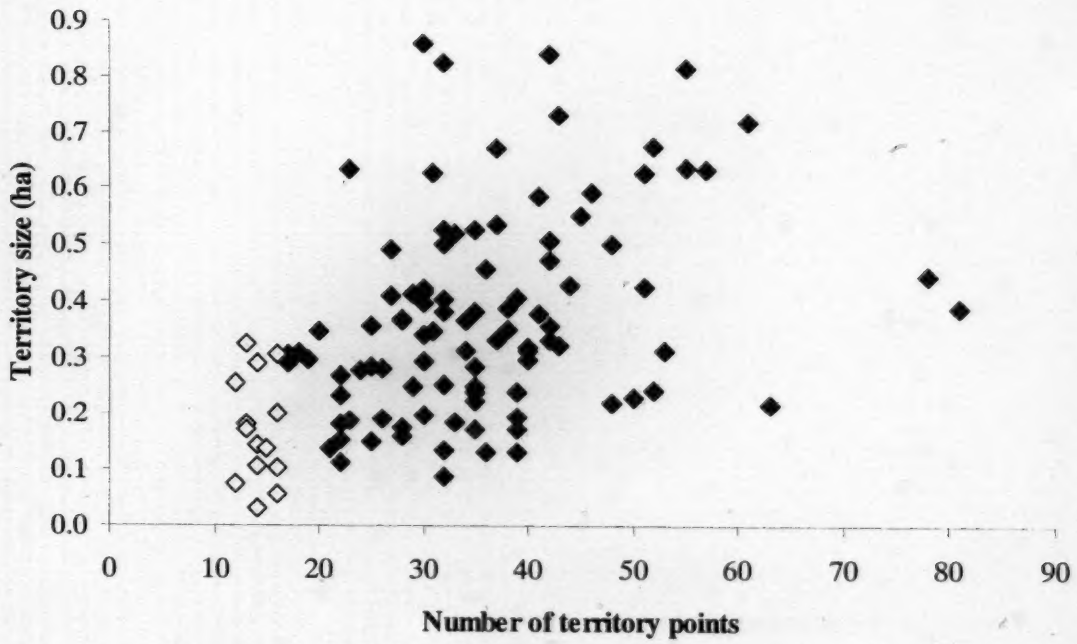
	Prop. Females breeding				Mean litter size				Prop. juveniles in t+1			
	Age-class				Age-class				Age-class			
Year	1	2	3	4	1	2	3	4	1	2	3	4
Population A												
1990	0.00	0.20	0.67	…	…	0.00	1.25	…	…	…	0.30	…
1991	0.00	1.00	0.83	1.00	…	0.00	1.40	1.75	…	…	0.57	0.57
1992	0.71	1.00	1.00	0.50	1.40	3.00	2.00	0.50	0.14	0.00	0.17	0.00
1993	0.67	1.00	…	1.00	3.00	3.00	…	1.00	0.50	0.67	…	0.67
1994	0.38	1.00	1.00	…	1.50	1.50	1.00	…	0.08	0.33	0.00	…
1995	1.00	0.80	1.00	…	1.50	1.50	2.67	…	0.33	0.61	0.38	…
1996	0.79	1.00	0.92	1.00	1.27	2.00	1.73	1.50	0.00	1.00	0.16	0.33
1997	0.00	0.58	0.90	1.00	…	0.57	1.78	1.00	…	0.50	0.38	0.00
1998	0.17	0.75	1.00	0.90	2.00	2.00	2.69	2.56	0.25	0.50	0.49	0.43
1999	0.51	0.83	1.00	0.57	1.44	1.40	1.25	1.75	0.08	0.00	0.05	0.00
2000	0.00	0.44	0.57	0.83	…	1.09	1.50	0.60	…	0.08	0.00	0.00
2001	…	1.00	1.00	1.00	…	2.00	2.11	1.50	…	0.50	0.13	0.00
2002	0.00	…	1.00	1.00	…	…	1.82	1.00	…	…	0.20	0.75
2003	0.00	1.00	1.00	0.75	…	1.00	1.00	2.00	…	0.00	0.00	0.00
Population B												
1990	0.00	0.40	0.68	…	…	0.00	1.23	…	…	…	0.50	…
1991	0.00	0.50	0.86	0.88	…	1.00	1.50	1.57	…	0.00	0.44	0.64
1992	0.73	0.75	1.00	0.89	1.38	0.67	4.25	2.63	0.00	0.00	0.06	0.14
1993	1.00	1.00	1.00	0.80	0.75	1.67	1.67	2.25	0.67	0.50	0.40	0.56
1994	0.47	1.00	0.83	1.00	2.33	2.67	2.00	0.50	0.10	0.00	0.10	0.00
1995	1.00	1.00	0.80	…	2.60	1.55	2.00	…	0.31	0.65	0.50	…
1996	0.43	0.50	1.00	1.00	1.44	2.50	2.20	2.50	0.08	0.00	0.14	0.00
1997	0.00	0.50	0.85	…	…	1.44	1.91	…	…	0.38	0.43	…
1998	0.91	1.00	0.88	1.00	1.60	2.00	1.87	2.75	0.50	1.00	0.54	0.18
1999	0.48	0.75	1.00	0.86	1.17	1.50	1.27	1.67	0.00	0.00	0.07	0.00
2000	0.00	0.09	0.50	0.40	…	1.00	1.33	2.00	…	1.00	0.00	0.00
2001	0.50	1.00	0.93	1.00	1.00	1.00	1.62	1.33	0.00	0.00	0.19	0.00
2002	0.00	1.00	1.00	1.00	…	2.00	2.00	1.00	…	0.00	0.33	0.00
2003	0.67	1.00	1.00	1.00	2.00	3.00	1.00	1.50	0.25	0.00	0.50	0.00



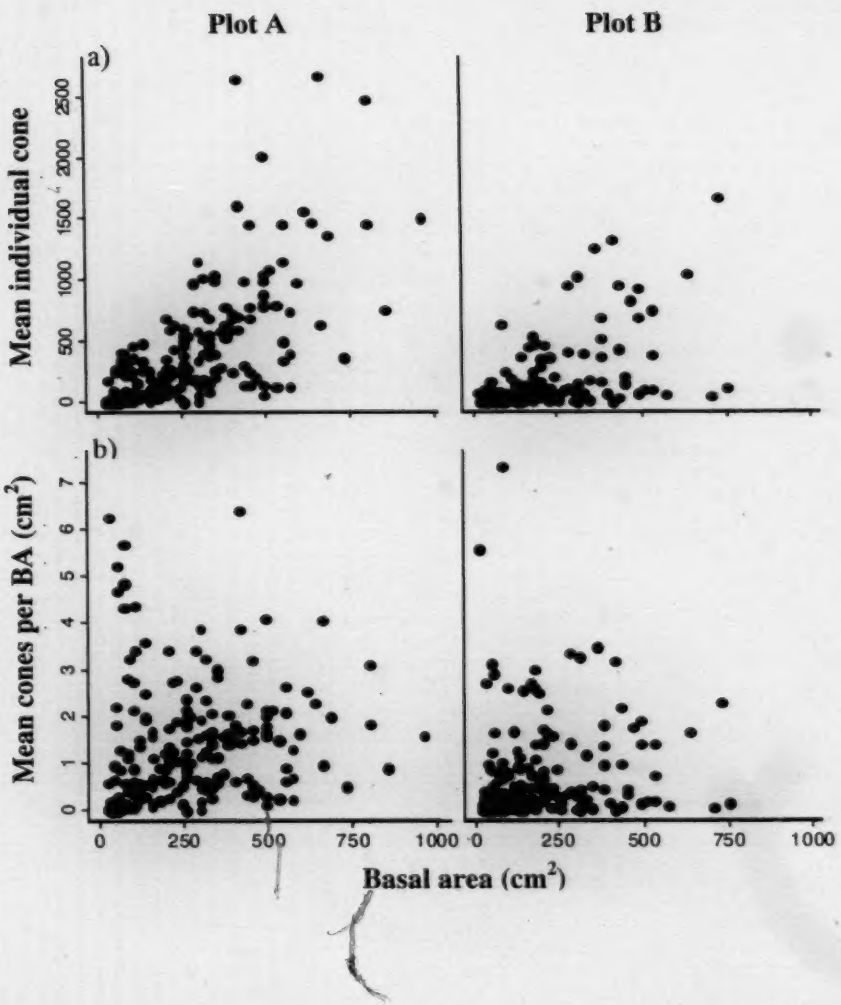
Appendix 3: Predicted (grey symbols) and observed (black symbols) red squirrel population growth rates for two populations in the Yukon, Canada, from 1990-2004. Predictions were based on models including a) population density only (DD), b) food only (F), and c) both food and population density (DD+FL).



Appendix 4: The mean correlation index (± SE) showing the proportion of variation in *P. glauca* individual cone production patterns that was explained by cone production on another tree within a given distance class (see text for further information).



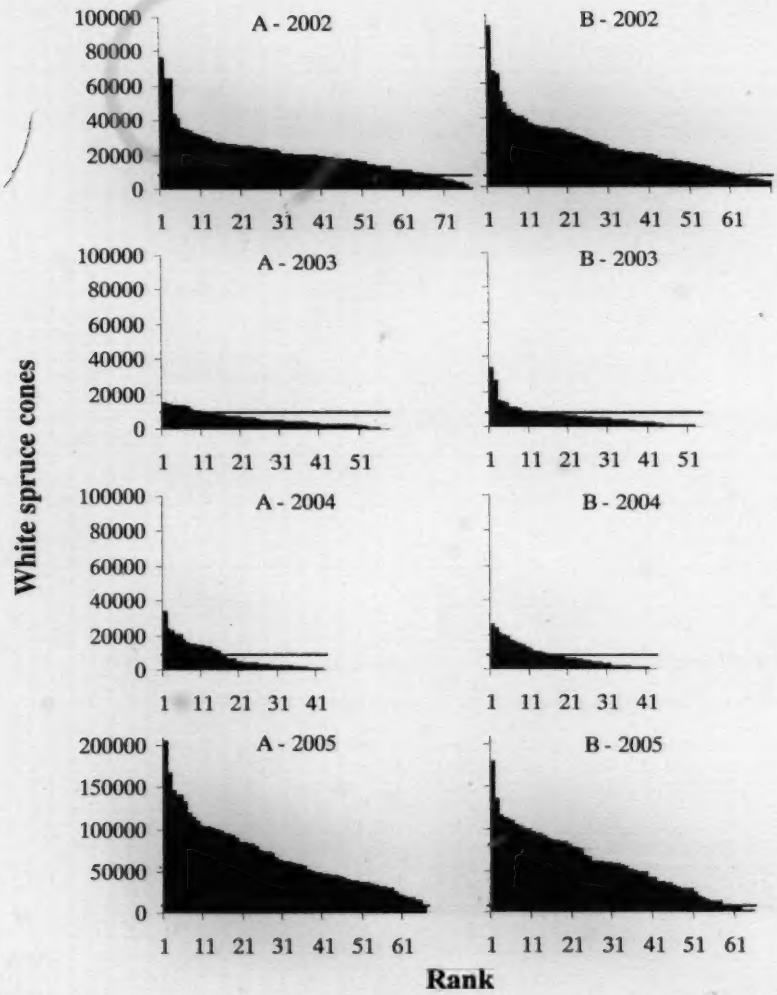
Appendix 5: Relationship between the number of territorial location points used to construct red squirrel territories and the resulting territory size (n = 112) for analyses in Chapter 6. Solid symbols are for territories with ≥ 17 data points, open symbols have <17 data points. Only territories mapped with a minimum of 17 points are discussed in the text and used in analyses.



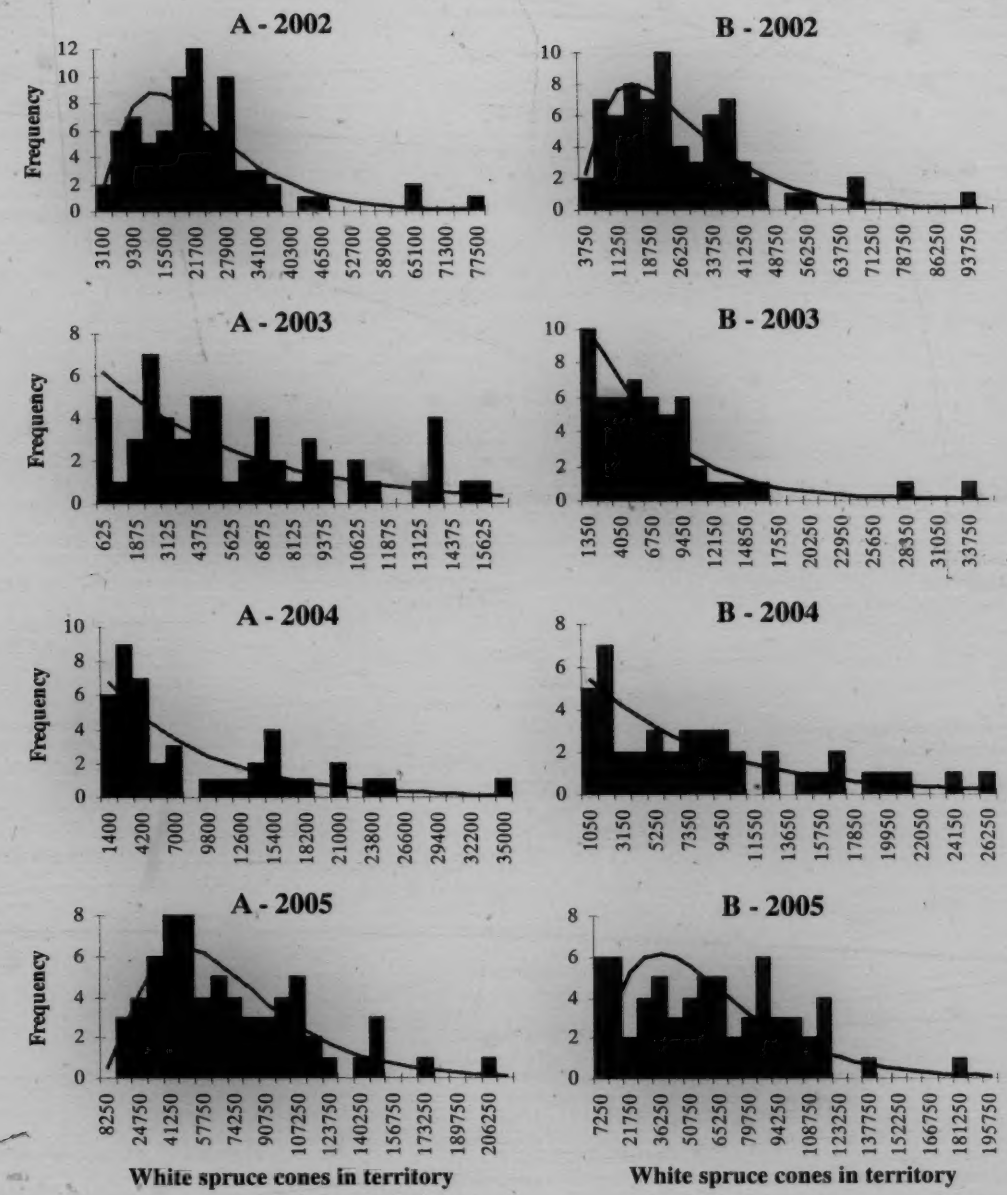
Appendix 6: a) Top panels show the trend of increases in mean individual white spruce cone production with increased basal area (2002-2005) in plots A (n = 207) and B (n = 261), and the high variability in cone production across the range of basal areas. b) Bottom panels show that there is little relationship between cone production per unit basal area and the basal area of the tree, this is especially the case for individuals with basal areas > 64cm^2 (9 cm dbh).

Appendix 7: Summary of territory size and number of cones in August territories of juveniles, adult males, and adult female red squirrels. Females are separated into non-breeders, those that bred but had no juveniles wean from the nest (failed breeders), and females who successfully weaned at least one offspring during the year. Means (standard errors) of raw and ln-transformed data are shown, with ranges of values in italics.

	Juveniles	Adult Males	Adult Females		
	(both sexes)		Non-breeder	Failed breeder	Weaned offspring
	(n = 19)	(n = 29)	(n = 16)	(n = 13)	(n = 16)
Territory size (ha)	0.22 (0.02)	0.41 (0.03)	0.50 (0.05)	0.43 (0.05)	0.33 (0.04)
	(0.09 - 0.38)	*(0.18 - 0.86)*	*(0.24 - 0.83)*	*(0.19 – 0.84)*	*(0.13 - 0.53)*
ln(territory size in m^2)	7.63 (0.09)	8.25 (0.07)	8.44 (0.01)	8.30 (0.12)	7.99 (0.13)
	(6.80 - 8.23)	*(7.51 - 9.06)*	*(7.79 - 9.02)*	*(7.53 – 9.04)*	*(7.17 - 8.57)*
Territory cones	4,236 (1,337)	8,694 (1,531)	9,256 (1,921)	12,986 (2,887)	10,340 (3,291)
	(61 – 19,902)	*(269 – 29,418)*	*(205 – 27,432)*	*(824 – 34,644)*	*(440 – 52,613)*
ln(territory cones)	7.63 (0.09)	8.51 (0.23)	8.68 (0.30)	9.00 (0.33)	8.69 (0.28)
	(4.11 - 9.90)	*(5.60 - 10.29)*	*(5.32 - 10.22)*	*(6.71 – 10.45)*	*(6.09 - 10.87)*



Appendix 8: Rank of white spruce cone abundance within red squirrel territories based on the age-class of the primary midden owner and the cone density in 0.1ha surrounding the midden. Populations were in two study plots (A & B), and experienced three low cone years (2002-2004) and one mast year (2005). Y-axes are the estimated cones within each territory, note that 2005 is on a different scale; X-axes are the rank of cone abundance and vary due to fluctuations in population size. The horizontal line is at 7300 cones, half of the estimated overwinter energy requirement (Humphries et *al.* 2005; Chapter 6).



Appendix 9: Fit of gamma or exponential distributions (lines) to the number of cones in red squirrel territories (bars). Exponential distributions are shown for A-2003, A-2004, and B-2004, the remainder are gamma distributions.